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LIFE HISTORY PATTERNS IN MARINE FISHES AND THEIR CONSEQUENCES FOR FISHERIES MANAGEMENT

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ABSTRACT

Natural selection operates at the life history level to maximize the number of surviving offspring. Life history characteristics will vary in consistent patterns to meet this constraint. When theoretical patterns in life histories were investigated in terms of r and K selection and compared with actual trends in life history characteristics of fishes, the agreement between observed and predicted trends was significant. The effects of harvesting on stocks with these life history trends were investigated and it was found that K selected type species would be highly sensitive to overfishing and, once depleted, recovery would require a long time.

The ecological and genetic properties of a species are intimately linked. The morphological and reproductive characteristics, population sizes, and genetic frequencies of species are adjusted to their environments by natural selection. Species inhabiting different environments show different patterns of life history characteristics. The relationship among habitat, ecological strategies, and population parameters has been termed r and K selection (MacArthur and Wilson 1967) and/or optimal life histories (Gadgil and Bossert 1970). This body of theory is based on the assumption that natural selection operates on these characteristics in order to maximize the number of surviving offspring produced. Under an environmental regime with a large component of unpredictable, nonselective, mortality an organism will allocate a larger portion of its resources to reproductive activities (an r strategist). Conversely the optimal allocation of resources for a population subjected to a high proportion of predictable, selective mortality will be toward increasing individual fitness, frequently through competitive ability (a K strategist). With the number and variability of factors operating on any particular species, no species is going to be an r or K strategist in an absolute sense. A species will only occupy a relative position on the r and K continuum.

In fisheries biology, the value of comparative studies of life history parameters has long been recognized (Holt 1962; Beverton 1963; Cushing 1971; Alverson and Carney 1975). These life history parameters should vary in a consistent pattern which can be predicted from the theory of r and K selection. In this paper, these predictions are tested with life history parameters from major groups of marine fishes. The theory has implications for management, particularly when fisheries are in the initial stages of development.

THEORY OF r AND K SELECTION

The theory of r and K selection is based on two assumptions about the allocation of a population's resources between competitive and reproductive functions (Pianka 1974; Gadgil and Bossert 1970; Schaffer and Gadgil 1975). The first is that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. The second assumption is that any species only has a fixed amount of resources available. This results in an inverse relationship between the number of offspring produced and their average fitness. The criterion for success in natural selection is the number of surviving offspring that a parent produces (Crow and Kimura 1970). Therefore, the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible total number of offspring (r selection), and production of offspring with the highest possible fitness (K selection). The particular point of compromise for any species will be a function of the selection factors operating on that species and would be that species' position on the r and K continuum.

The second part of the theory concerns the relationship between these life history strategies and

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the habitat the species occupies (Southwood et al. 1974; Southwood and Comins 1976). If mortality factors in an environment are variable and/or unpredictable, then their effects are likely to be less selective in terms of population size or of the phenotype involved. Under these circumstances, individual competitive fitness is of relatively less importance. The best strategy would be to place maximal resources into reproduction and produce as many offspring as possible (*r* selection).

The contrasting situation is an environment in which mortality factors are stable and/or predictable. Mortality under these circumstances will result in strong selection for individual fitness and there will be pronounced differences between their effects on different phenotypes. In these stable environments, the optimal strategy would be to produce offspring with substantial competitive ability (*K* selection). Due to the previously assumed relationship between fitness per offspring and the number of offspring produced, this also means the production of fewer offspring.

The two situations described above are end points of a spectrum. Species will always have a number of different selective pressures operating on them, both spatially and temporally. This is particularly evident in aquatic organisms which characteristically go through several life history stages. This again emphasizes that the concept of *r* and *K* selection should be applied only in a comparative sense. Finally, comparisons must be made between species of a similar ecological nature. Comparisons between species of different ecological types is meaningless since fundamentally different types of selective factors will be operating in those cases.

r AND *K* SELECTION IN MARINE FISHES

Natural selection will favor nonreproductive activities at the expense of reproductive activities only when they enhance reproduction at later stages in the life history and thereby maximize overall survival (Crow and Kimura 1970). Changes in allocation of a species' resources from reproductive to competitive activities will only occur in habitats where competitive activities enhance the survival of future offspring. The result of this is that organisms under different selection pressures will have characteristic life history patterns. An *r* selected species will have life history strategies which tend toward productivity. The *K* selected species will have life strategies which tend toward efficient exploitation of a specific limiting resource (Pianka 1974). Therefore, specific combinations of population parameters can be identified as being characteristic of an *r* strategist, while the opposing combination would be characteristic of a *K* strategist.

A species which is exposed to a large component of nonselective or catastrophic mortality (i.e., an *r* strategist) would be selected for characteristics that would increase productivity. Increasing productivity through reproductive activity generally implies: 1) early maturity, 2) rapid growth rates, 3) production of larger numbers of offspring at a given parental size, and 4) maximum production of offspring at early age (Gadgil and Bossert 1970). Other characteristics which are results of the allocation of large portions of resources to reproductive activity are: 1) small body size, 2) high rates of mortality, and 3) shorter life span (Pianka 1974; Gadgil and Solbrig 1972). In terms of commonly measured population parameters in fishery biology, an *r* selected species would have: 1) a low age at first maturity, 2) a high value of *k* from the von Bertalanffy growth equation, 3) a small L_∞ from the von Bertalanffy growth equation, 4) high rates of instantaneous natural mortality (*M*), and 5) low maximum age.

Even in environments with predictable mortality sources, increased allocation of resources to competitive activities will only occur when two prerequisites are met (Schaffer and Gadgil 1975). The first is that reproductive potential increases with some function of age. The second is that there is some additional mortality risk associated with reproduction. Under these assumptions, the attributes associated with a *K* strategist would be: 1) delayed maturity, 2) reduced growth rates, 3) low mortality rates, 4) large body size, and 5) longer life span. Again in terms measured in fishery biology, a *K* selected species would have: 1) a high age at first maturity, 2) a low *k* from the von Bertalanffy growth equation, 3) a large L_∞ from the von Bertalanffy growth equation, 4) low *M*, and 5) a high maximum age.

Using these life history correlates of *r* and *K* selection (summarized in Table 1), it is possible to predict the signs of a correlation matrix between life history parameters (Table 2). The predicted matrix can be compared with actual matrices calculated using Spearman's rank correlation coefficient. This coefficient only assumes that the observed data are mutually independent and come

TABLE 1.—Summary of hypothetical *r* and *K* correlates in life history parameters of fishes.

Characteristics	*r* selected	*K* selected
Body size, L_∞[1]	Small	Large
Maximum age	Low	High
Age at first maturity	Low	High
Natural mortality, *M*	High	Low
Growth rate, *k*[1]	High	Low

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 2.—Predicted signs of correlation matrix of life history parameters in fishes.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	*k*[1]
Body size, L_∞[1]	1.0	+	+	–	–
Maximum age		1.0	+	–	–
Age at first maturity			1.0	–	–
Natural mortality, *M*				1.0	+
Growth rate, *k*[1]					1.0

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

from a continuous bivariate population (Hollander and Wolfe 1973).

RESULTS

Life history parameters were gathered from the literature for several major groups of marine fishes. Often there were multiple sets of data for the same species from different locations. Each set of values was used as a separate data case. The literature citations for the actual parameters are listed by group in Appendix I. Correlation matrices were calculated for the following groups of fish: 1) herring and anchovies, Clupeidae and Engraulidae (Table 3), 2) salmons, Salmonidae (Table 4), 3) cods, Gadidae (Table 5), 4) rockfishes, Scorpaenidae, genus *Sebastodes* (Table 6), and 5) flatfishes, Pleuronectiformes (Table 7).

All of the observed correlations agree with the predicted correlations in sign (Table 8). Of the observed correlations, 40 of a possible 46 (or 87%) were significantly different from zero at a 5% probability level. If the observed correlation agreement of coefficients were distributed ran-

TABLE 3.—Correlation coefficients between life-history parameters for herring and anchovies (families Clupeidae and Engraulidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	*k*[1]
Body size, L_∞[1]	1.0	0.846 (0.001)	0.816 (0.001)	−0.746 (0.001)	−0.720 (0.001)
Maximum age		1.0	0.904 (0.001)	−0.797 (0.001)	−0.763 (0.001)
Age at first maturity			1.0	−0.702 (0.001)	−0.732 (0.001)
Natural mortality, *M*				1.0	0.876 (0.001)
Growth rate, *k*[1]					1.0

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 4.—Correlation matrix between life-history parameters for salmons (family Salmonidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	*k*[1]
Body size, L_∞[1]	1.0	0.765 (0.001)	0.728 (0.032)	−0.785 (0.001)	−0.730 (0.002)
Maximum age		1.0	0.776 (0.020)	−0.737 (0.003)	−0.674 (0.004)
Age at first maturity			1.0	−0.644 (0.084)	−0.812 (0.013)
Natural mortality, *M*				1.0	0.896 (0.001)
Growth rate, *k*[1]					1.0

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 5.—Correlation matrix between life-history parameters for cods (family Gadidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*M*	*k*[1]
Body size, L_∞[1]	1.0	0.795 (0.002)	0.833 (0.001)	−0.647 (0.022)	−0.666 (0.001)
Maximum age		1.0	0.737 (0.014)	−0.654 (0.028)	−0.702 (0.008)
Age at first maturity			1.0	−0.715 (0.035)	−0.658 (0.008)
Natural mortality, *M*				1.0	0.950 (0.001)
Growth rate, *k*[1]					1.0

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 6.—Correlation matrix between life-history parameters for rockfishes (family Scorpaenidae, genus *Sebastodes*). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	*k*[1]
Body size, L_∞[1]	1.0	0.662 (0.019)	0.456 (0.088)	−0.490 (0.075)
Maximum age		1.0	0.612 (0.030)	−0.567 (0.040)
Age at first maturity			1.0	−0.651 (0.021)
Growth rate, *k*[1]				1.0

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 7.—Correlation matrix between the life-history parameters for flatfishes (order Pleuronectiformes). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	0.755 (0.001)	0.956 (0.001)	0.291 (0.156)	-0.619 (0.005)
Maximum age		1.0	0.824 (0.001)	-0.355 (0.142)	-0.808 (0.001)
Age at first maturity			1.0	-0.630 (0.014)	-0.732 (0.001)
Natural mortality, M				1.0	0.367 (0.098)
Growth rate, k[1]					1.0

[1] The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 8.—Summary of the number of agreements between predicted and observed correlation coefficients among life-history parameters within selected taxonomic groups.

Level of agreement	Number in agreement	Number possible	Percent in agreement
Sign	46	46	100
5% probability level	40	46	87
1% probability level	31	46	67

domly (i.e., p = probability of agreement = 0.5, and q = probability of disagreement = 0.5), then the number of agreements would follow a binomial distribution. The binomial test (Hollander and Wolfe 1973) can be used to test the hypothesis that the number of agreements between the predicted and observed correlations differs from the number that would have occurred randomly. The number of agreements is significantly different than would have occurred randomly ($z = 4.86$, $P<0.001$), when only correlations that were significant at the 5% level were used.

RESPONSE OF *r* AND *K* SELECTED SPECIES TO HARVESTING

The interaction of life history characteristics will have a strong affect on the response of a species to fishing pressure. The Beverton and Holt yield per recruit equation estimates the yield that can be harvested from the growth of a cohort. The model assumes that fish growth is described by the von Bertalanffy growth curve and that mortality processes are exponential (Beverton and Holt 1957; Ricker 1975). The biological parameters in the model are: 1) M, the instantaneous rate of natural mortality, 2) W_∞, the mean asymptotic weight which corresponds to L_∞, 3) k, the von Bertalanffy growth coefficient, and 4) t_λ, the maximum age of a fish. From r and K selection, we can predict how these parameters will vary. Consider a situation with three hypothetical species: one species will be more r selected, another species will be more K selected, and another will be intermediate between the first two. The biological parameters will vary as shown in Table 9. Beverton and Holt yield per recruit curves were calculated for a constant age at first capture ($t_r = 4.2$ yr) with varying fishing mortality (Figure 1), and for a constant fishing mortality ($F = 0.25$) with a varying age at first capture (Figure 2).

The yield per recruit analysis points up that there are specific differences in fisheries based on r or K selected species. In fisheries based on K selected species, the maximum yield per recruit would occur at a lower level of fishing mortality and at a later age at first entry than in fisheries based on r selected species. The curves also indicate that K selected species would be much more sensitive to overfishing both in terms of fishing mortality and age at first entry.

The surplus production model of Schaefer combines reproductive and mortality functions into one parameter (Ricker 1975). The biological parameters in this model are B_∞, the maximum stock size (or carrying capacity in weight), and k, the instantaneous rate of increase of the stock at densities approaching zero. Again these parameters can be predicted for the three hypothetical species from r and K selection (Table 10). In the surplus production model analysis (Figure 3), the r selected species have the highest productivity. As in the yield per recruit analysis, the maximum yield occurs at a lower fishing mortality for the K

TABLE 9.—Biological parameters for use in yield per recruit analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Natural mortality, M	0.30	0.20	0.10
Mean asymptotic weight, W_∞	641 g	1,141 g	1,641 g
von Bertalanffy growth coefficient, k	0.22	0.14	0.07
Maximum age, t_λ	13 yr	20 yr	35 yr

TABLE 10.—Biological parameters for surplus production model analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Maximum stock size (B_∞)	1.54×10^8g	2.04×10^8g	2.54×10^8g
Rate of increase (k)	0.912	0.612	0.312

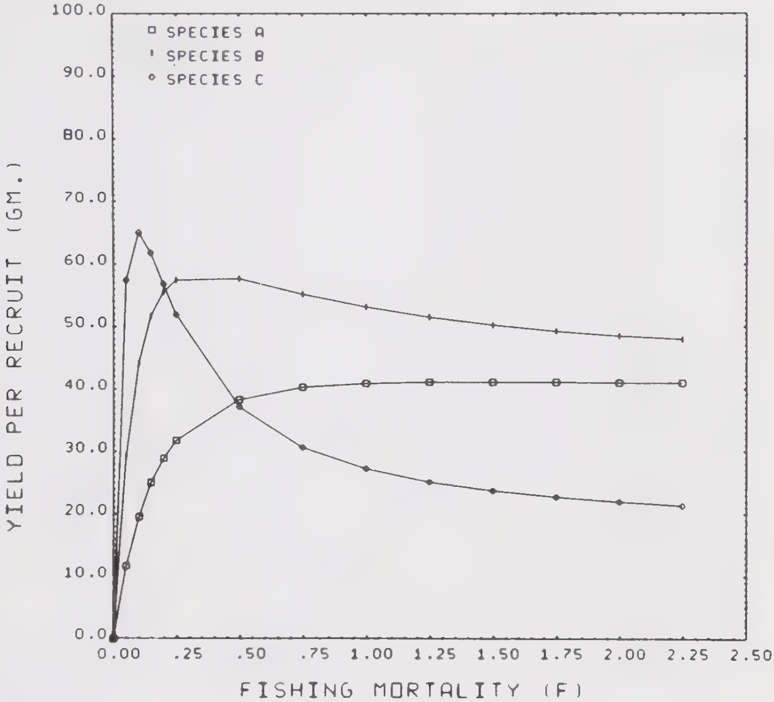

FIGURE 1.—The effect of different levels of fishing mortality with constant age of recruitment (4.2 yr) on yield per recruit of three hypothetical fish species demonstrating the range of *r* and *K* selection.

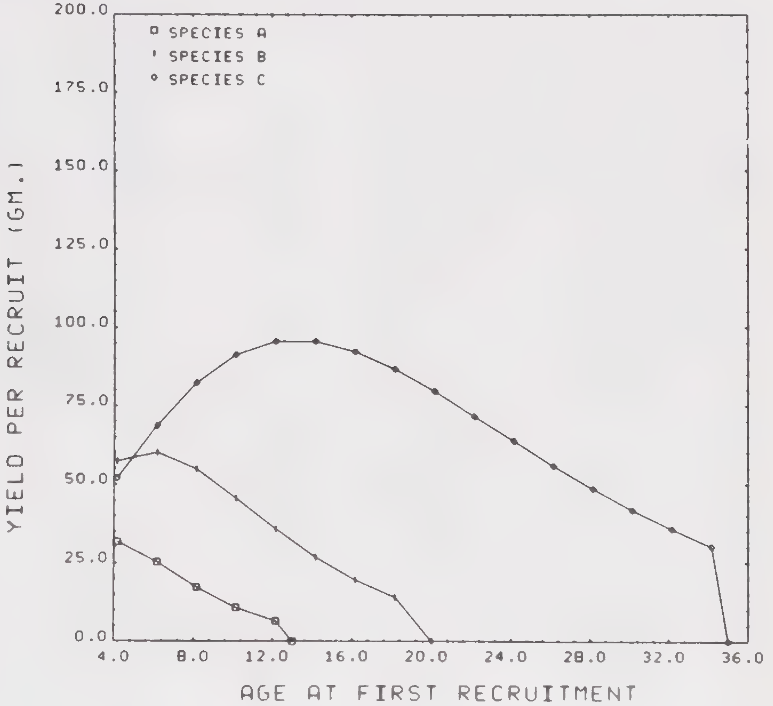

FIGURE 2.—The effect of different mean ages of recruitment at constant fishing mortality ($F = 0.25$) on yield per recruit of three hypothetical fish species demonstrating the range of *r* and *K* selection.

selected species than for the *r* selected species. The *K* selected species is reduced to levels lower than the maximum sustainable yield by overfishing much more rapidly than the *r* selected species.

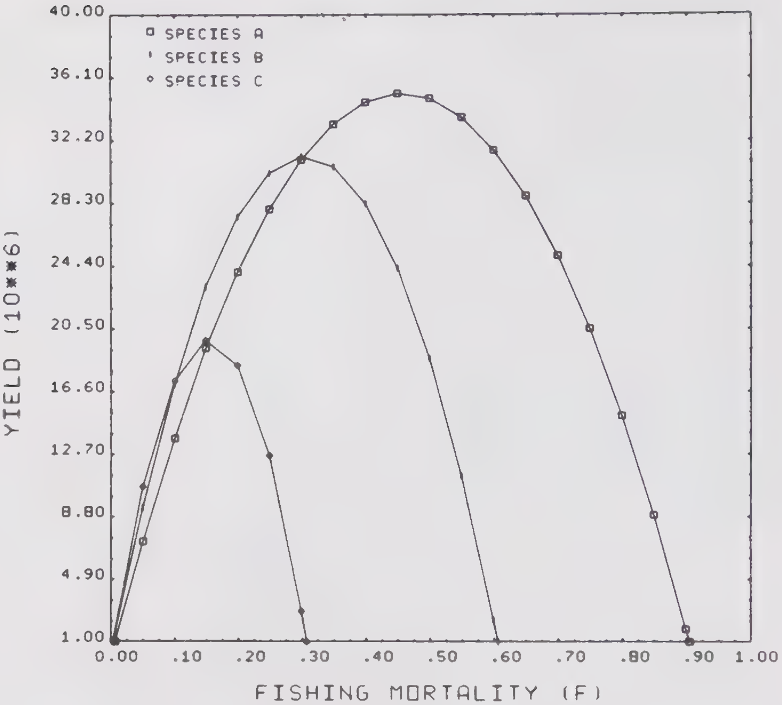

FIGURE 3.—Maximum equilibrium yields (× 10^6 g) from Schaefer surplus production curves as a function of fishing mortality for three hypothetical fish species demonstrating the range of *r* and *K* selection.

DISCUSSION

Life history parameters vary in consistent patterns. These patterns are explainable and predictable by the theoretical constructs of *r* and *K* selection. This is not a particularly new or unique idea in fisheries biology. Beverton and Holt (1959) investigated a positive relationship between body size and life span and between mortality and growth rates. Cushing (1971) suggested that there is a negative relationship between degree of density dependent regulation and fecundity. Alverson and Carney (1975) have suggested a positive relationship between body size and the time when a cohort maximizes its biomass. In population ecology, similar relationships have been investigated for zooplankton (Allan 1976), plants (Gadgil and Solbrig 1972; MacNaughton 1975), and animals (Smith 1954; Bonner 1965). All these empirical observed trends in life history parameters, along with the trends described here, are consistent with *r* and *K* selection.

It is important to reemphasize here the comparative nature of *r* and *K* selection. The *r* and *K* continuum is a model and as such occurs only in an idealized sense. The idealized *r* selected species occurs in an ecological vacuum with no density effects and no competition. The idealized *K* selected species occurs in a completely saturated ecosystem where densities are high compared with carrying capacities and competition for resources is intense. The problem of applying this model to any real situation is not a trivial one. Species are not simply subjected to a single selective pressure, or even to a single set of selective pressures. Because of this, *r* and *K* concepts should only be applied in a comparative sense between groups of species that have some degree of functional similarity. No species is *r* selected or *K* selected in an absolute sense; it is only relatively more *r* selected or *K* selected than some other reference species. This theory will only have value in a situation where the population dynamics of one member of a species group are fairly well understood.

The results of the model analysis give several indications about the reaction to harvesting pressure of species which are more or less *r* or *K* selected. Fisheries based on more *r* selected species will be more productive. They can be fished at younger ages and at higher levels of fishing mortality. Given a minimum population size, these fisheries should also have a quicker recovery from overfishing. Species which are more *r* selected are likely to be strongly influenced by physical forces in the environment (Pianka 1974). Relationships of this type, e.g., between anchovies and upwelling, should be important considerations in management plans for these species.

Fisheries based on more *K* selected species will have a high maximum yield per recruit, but there will be fewer fish. Maximum equilibrium yield will occur at later ages of entry into the fishery and at lower levels of fishing mortality. These fisheries would be more susceptible to overfishing and stock depletion. Besides these species' sensitivity to overfishing, more *K* selected species are much more likely to have sophisticated life history mechanisms (Pianka 1974) which would have to be recognized in a management plan. These mechanisms might include parental care systems such as nesting or live births, mating systems, or territoriality. The more *K* selected species are much more likely to have strong interspecific relationships, usually competitive ones. The relationship between competition and harvesting has been dealt with by Larkin (1963) and Tanner (1975). Additional density independent mortality (fishing mortality) increases the advantage for the population with a higher population growth rate (i.e., more *r* selected). Therefore, even low levels of fishing pressure can destabilize a previously stable competitive pair and result in decline of the harvested species. Interestingly, the opposite result is also possible; harvesting pressure can stabilize a previously unstable species pair as Slobodkin (1962) found with experimental populations of hydra.

Fisheries based on more *r* selected species are likely to be of a boom and bust nature. Although in some years catches in these fisheries will be very large, they will be characterized by erratic production levels. The most efficient form of harvesting these fisheries will be fleets which are capable of switching between a number of target species relatively quickly.

Fisheries based on more *K* selected species, in contrast to the boom and bust nature of *r* selected fisheries, will be characterized by relatively stable population sizes and therefore catch levels. Given some initial measure of year class strength, possibly through larval or prerecruitment surveys, the prediction of future catches from that fishery could be made with a fair degree of accuracy. However, once fisheries based on these species become overfished, it would require a long period for the stock to rebuild to levels which can support economical profitable fisheries. An extremely *K* selected species would only be suitable for trophy fisheries.

Fisheries based on *r* and *K* selected species have been discussed in a comparative sense, but predation (in the case of a fishery, human predation) will also have effects on an individual species. The gene pool of any species is going to contain within it some range of variation of both *r* and *K* selected traits. The effects of increasing fishing mortality, which is assumed to be density independent (Cushing 1975), on life history characteristics has been theoretically analyzed by Roughgarden (1971). The general effect is an increase in selective advantage for the *r* selected proportions of the gene pool. This would mean an increase in growth rates, reduced age at first maturity, and greater fecundity at age. These trends will be more conspicuous in species that are relatively more *K* selected. Species that are more strongly *r* selected are likely to have less range of variation in this direction. One example of these effects of predation pressure is a comparison of lake trout, *Salvelinus namaycush*, populations under heavy predation pressure from the freshwater harbor seal, *Phoca vitulina*, to populations in nearby lakes without seals (Power and Gregoire 1978). The lake trout populations which were preyed upon by seals had faster growth rates, small maximum body size, reduced maximum age, lower age at sexual maturity, and greater individual fecundity compared with populations in lakes without seals. Growth and maturation rates of certain seal species have also increased where populations have been reduced by fisheries (Sergeant 1973). These affects can be attributed to changes in selection pressure resulting from sustained harvesting.

In summary, *r* and *K* selection seems to have been an important evolutionary trend on marine fish populations. The basic hypotheses are confirmed by the data presented here. The result of patterns in population parameters which arise from *r* and *K* selection is that different management strategies would be appropriate. The value of this approach is likely to be in initial stages of development of a fishery. As a fishery becomes more developed and more specific information becomes available, a more refined management strategy would become possible.

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APPENDIX I: LITERATURE CITATIONS FOR POPULATION PARAMETERS BY SPECIES

Herring and Anchovies, Families Clupeidae and Engraulidae

Clupea harengus—Lea 1919; Sund 1943a, b; Jensen 1947; Fridriksson 1950, 1951-61; Alander 1950; Tibbo 1956, 1957a, b; Hannerz 1956; Gilis 1957-61; Smith 1957; Day 1957; Cushing 1959; Nielsen 1960; Burd 1962; Parrish and Craig 1963; Postuma 1963; Bowers 1963.

C. pallasii—Hanamura 1953; Tester 1955; Ricker 1958; Tanaka 1960; Ayushin 1963; Motoda and Hirano 1963.

Sprattus sprattus—Robertson 1938; Molander 1943; Faure 1950; Elwertowski 1957-60.

Sardinops caerulea—Silliman 1943; Phillips 1948; Mosher and Eckles 1954; Clark and Marr 1955; Murphy 1966; Culley 1971.

S. melanosticta—Tanaka 1960; Tokai Regional Fisheries Research Laboratory 1960.

S. neopilchardus—Blackburn 1950.

S. ocellata—Davies 1958; De Jager 1960; Culley 1971.

Sardina pilchardus—Hodgson and Richardson 1949; Bough 1952; Hodgson 1957; Larrañeta 1960; Cushing 1961; Culley 1971.

Sardinella aurita—Postel 1955; Rossignol 1955; Richardson et al. 1960; Ben-Tuvia 1960; Beverton 1963.

S. longiceps—Nair 1960.

Engraulis encrasicholus—Fage 1920; Furnestin 1945.

E. japonicus—Hayashi and Kondo 1957; Watanabe 1958; Tanaka 1960; Hayashi 1961.

E. mordax mordax—Clark and Phillips 1952; Miller et al. 1955; Miller and Wolf 1958; Culley 1971.

Cetengraulis mysticetus—Barrett and Howard 1961.

Salmons, Family Salmonidae

Coregonus clupeaformis—Hart 1931; Hile and Deason 1934; Kennedy 1943, 1953; Ricker 1949.
Cristivomer namaycush—Kennedy 1954.
Leucichthys artedii—Hile 1936.
L. kiyi—Deason and Hile 1947.
Oncorhynchus kisutch—Shapovalov and Taft 1954; Drucker 1972.
O. nerka—Foerster 1968; Van Cleve and Bevan 1973.

Cods, Family Gadidae

Boreogadus saida—Beverton and Holt 1959.
Gadus callarias—Beverton and Holt 1957; Taylor 1958.
G. macrocephalus—Ketchen 1964.
G. minutus—Menon 1950.
G. morhua—Fleming 1960; Pinhorn 1969; Clayden 1972.
G. virens—Beverton and Holt 1959.
Melanogrammus aeglefinus—Raitt 1939; Beverton and Holt 1957.
Merluccius merluccius—Beverton and Holt 1959.

Rockfishes, Family Scorpaenidae, Genus *Sebastodes*

Sebastodes crameri—Phillips 1964.
S. diploproa—Phillips 1964.
S. entomelas—Phillips 1964.
S. flavidus—Phillips 1964.
S. goodei—Phillips 1964.
S. jordani—Phillips 1964.
S. miniatus—Phillips 1964.
S. paucispinis—Phillips 1964.
S. pinniger—Phillips 1964.
S. saxicola—Phillips 1964.

Flatfishes, Order Pleuronectiformes

Citharichthys sordidus—Arora 1951.
Eopsetta jordani—Ketchen and Forrester 1966.
Hippoglossus platessoides—Powles 1965, 1969; MacKinnon 1973.
H. vulgaris—Beverton and Holt 1959.
Isopsetta isolepis—Hart 1948.
Pleuronectes platessa—Beverton and Holt 1959.
Pseudopleuronectes americanus—Dickie and McCracken 1955.
Solea vulgaris—Beverton and Holt 1957.

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Morphology and Distribution Patterns of Several Important Species of Rockfish (Genus *Sebastes*)

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Introduction

In central California, commercial catches of rockfish (genus *Sebastes*) are dominated by bocaccio, *Sebastes paucispinis*, and chilipepper, *S. goodei*. As one moves northward, composition of the commercial catch gradually changes, and in northern Washington, the catch is dominated by Pacific ocean perch, *S. alutus;* silvergray rockfish, *S. brevispinis;* yellowtail rockfish, *S. flavidus;* and canary rockfish, *S. pinniger*. Because of the possibility of a fishery for smaller rockfish species, shortbelly rockfish, *S. jordani*, can also be included in this north-south grouping of commercial species (Table 1).

Table 1.—Commercial rockfish species.

Southern species	Northern species
Chilipepper	Pacific ocean perch
Bocaccio	Silvergray rockfish
Shortbelly rockfish	Yellowtail rockfish
—	Canary rockfish

Several of these commercially important species are very similar in appearance, particularly the Pacific ocean perch and chilipepper and the silvergray rockfish and bocaccio. This similarity in appearance is significant since studies on habitat utilization of fishes with similar feeding morphologies suggest that spatial segregation is probably one of the most important means of niche separation (Werner and Hall, 1977). It is also important because similarity in feeding morphology suggests a similarity in the basic adaptive strategy of these species.

Morphological Relationships

Morphological measurements for these species were taken from Phillips (1957). Variables were chosen which were characteristic of a species' basic adaptive strategy. They include length of head, length of upper jaw, orbit diameter, least depth of caudal peduncle (all as ratios to standard length), the ratio of body height/body width, both at pectoral fins, and maximum recorded length (Table 2).

The first three variables will strongly affect a species' feeding behavior. A species' height/width ratio and depth of caudal peduncle are measures of the hydrodynamic qualities of a fish. The fusiform body, moderately elliptical in cross section, is physically the most efficient for movement through a liquid medium, and therefore is characteristic of species that swim more or less continuously. Species that are in constant motion are also characterized by a narrow caudal peduncle and deeply incised caudal fin (Alexander, 1967). Maximum length was included both because of its effect on movement and because of the effect of absolute size on predation dynamics (Wilson, 1975). The species were clustered using a phi-squared distance coefficient (Sneath and Sokal, 1973). The dendrogram (Fig. 1) shows that species are grouped into a number of species pairs.

Silvergray rockfish and bocaccio are relatively large fish with a large head size and a large jaw size. They also have, relative to the other species, a much smaller orbit. Their body shapes are compressed fusiform and they have moderately incised caudal fins. Bocaccio is primarily piscivorous (Phillips, 1964), and the morphologies of these two species are strongly adapted for

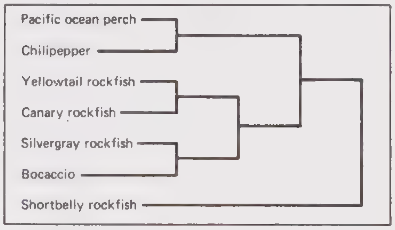

Figure 1.—Cluster analysis of morphological similarity of rockfish species.

ABSTRACT—This paper investigates some aspects of the relationship between morphology and distribution of some of the commercially important species of rockfish (genus Sebastes*). On the basis of morphometrics, several species pairs of rockfish are suggested. Members of the species pairs are found to be spatially segregated. It is suggested that certain types of adaptive strategies are very important in terms of species that can support commercial fisheries.*

Table 2.—Morphological variables for rockfish species (genus *Sebastes*).

Species	Length of head[1]	Length of upper jaw[1]	Orbit diameter[1]	Height/Width	Least depth of caudal peduncle[1]	Maximum length (cm)
Pacific ocean perch	0.370	0.169	0.103	1.97	0.086	50.4
Silvergray rockfish	0.370	0.189	0.080	2.00	0.090	71.1
Yellowtail rockfish	0.357	0.167	0.089	1.67	0.108	66.0
Chilipepper	0.357	0.159	0.085	1.97	0.084	55.9
Shortbelly rockfish	0.344	0.139	0.088	1.88	0.078	30.5
Bocaccio	0.370	0.200	0.074	2.00	0.086	91.1
Canary rockfish	0.357	0.178	0.091	1.97	0.114	76.4

[1] Ratio to standard length.

taking large mobile prey. The large body and mouth size are obvious adaptations for increased prey size. The smaller orbit diameter suggests a reduction in the importance of visual recognition. The large mouth also increases the angle at which a prey item can be taken by allowing the fish to grasp the prey at the side of its jaw (Alexander, 1967). In this way the fish does not have to be directly in front of a prey item for capture. The compressed fusiform body shape and the moderately incised caudal fin suggest an increase in acceleration at the cost of some efficiency in swimming. All of these characteristics show a high level of adaptation for the capture of large mobile prey items.

Pacific ocean perch and chilipepper are smaller fish with smaller mouth sizes. However, their orbit diameter, particularly Pacific ocean perch, is larger. Their body shape is also a compressed fusiform one, but with a more deeply incised caudal fin. These species feed primarily on pelagic crustaceans, particularly on euphausids (Phillips, 1964; Skalkin, 1964). The reduced mouth size is a reflection of the smaller prey size. It also reduces the angle at which the fish can take a prey. The more deeply incised caudal fin suggest a fish which is more efficient at cruising with some sacrifice in acceleration. The increased orbit diameter could imply that a smaller prey size increases the difficulty of visual recognition.

The shortbelly rockfish is the smallest of the species with by far the smallest mouth size. The body shape is a more rounded fusiform one with the smallest height/width ratio. The species also has the narrowest caudal peduncle and is the only species with a deeply incised caudal fin. The shortbelly rockfish feeds primarily on macroplankton (Phillips, 1964). The small mouth size is accompanied by a large orbit diameter. This suggests that prey items are small and even more difficult to see. The body shape is the most strongly adapted for efficient cruising. The shortbelly rockfish has no direct replacement as the other species pairs.

Yellowtail and canary rockfish were paired together primarily because they both have a much thicker caudal peduncle than the other species. However, they are not really similar species except for the fact that they are very different than the other species so far discussed. Also both of these species are members of the northern group of commercial species and have no apparent replacement in the southern group of commercially important species. Since these species represent a fundamentally different line of adaptive strategies, they will not be discussed further.

These species, except for yellowtail and canary rockfish, represent a morphological trend from a large fish with a larger mouth size to a small fish with a smaller mouth size. It is probable that the species also represent to some degree a trend in feeding types. The interesting point is the degree of apparent replacement of species in the transition from the southern to the northern complex.

Distributional Analysis

The similarity of the morphometrics of these species pairs implies that they should show some degree of spatial segregation (Werner and Hall, 1977). The data for this analysis came from the 1977 Rockfish Survey (Gunderson and Sample, 1980). Species densities (in pounds per nautical miles trawled) were calculated in 30-minute blocks of latitude. The data, by species, are shown in Table 3. Histograms were also constructed for the major species for densities combined over all depths (Fig. 2,3).

Association between species was measured from presence-absence data using the binary correlation coefficient, *V*. Sampling properties and test of significance are given in Pielou (1969). Table 4 gives values of *V* and their significance.

The histograms of Pacific ocean perch and chilipepper show a trend of a peak of abundance of the southern species, an area of overlap with reduced abundance of both species, and then a peak of abundance in the northern species. The correlation analysis between the species pair shows a strong negative association. The histograms of bocaccio and silvergray rockfish show an area of abundance of the southern species and an area of overlap. The correlation analysis shows a nonsignificant result. This probably is the result of using a presence-absence correlation technique. Use of the abundance

Table 3.—Rockfish species density (pounds per nautical mile) per 30-minute block.

Latitude		Pacific ocean perch	Silvergray rockfish	Yellowtail rockfish	Chili-pepper	Shortbelly rockfish	Bocaccio	Canary rockfish
Deg.	Min.							
34	0	0	0	0	1.7	4.4	5.6	0.3
	30	0	0	0.1	5.5	13.4	23.6	1.0
35	0	0	0	0	0.5	4.9	5.0	0
	30	0	0	0	20.2	31.0	3.2	0.1
36	0	0	0	26.4	0.1	7.4	28.6	0.2
	30	0	0	0	13.1	435.2	15.2	0.8
37	0	0	0	0	15.4	487.1	15.3	0.2
	30	0	0	0	118.5	0.9	269.2	11.9
38	0	0	0	0	99.6	55.0	14.4	0.3
	30	0	0	2.9	53.7	9.5	13.1	1.1
39	0	0.2	0	0.5	92.3	14.4	8.4	0.7
	30	0.1	0	4.2	78.7	1.2	7.6	1.0
40	0	0	0	0	10.7	0.1	1.8	21.5
	30	6.8	0	0	4.6	0	0.5	0
41	0	0.7	0	0.2	0	0	0	0.2
	30	1.1	0	0	0	0	0	0.4
42	0	2.6	0	0.3	0	0	0	0
	30	21.1	0	25.0	0.1	0	1.2	0.8
43	0	6.3	0	1.9	0	0	0.7	5.9
	30	10.9	0	2.2	0	0.1	0.8	0.3
44	0	15.5	1.0	0.2	0	0.7	2.6	3.8
	30	8.8	0	24.6	0	0	0.9	0.1
45	0	13.9	0.2	0.2	0	0	0.2	0.2
	30	23.9	0.3	1.5	0	0.1	1.6	28.8
46	0	101.6	8.6	75.6	0	0	17.9	48.8
	30	133.3	0	80.9	0	0	0.7	60.5
47	0	70.6	15.3	115.6	0	0	7.0	22.3
	30	33.5	10.2	26.1	0	0	0.7	1.1
48	0	180.6	193.3	141.1	0	0	22.8	276.9

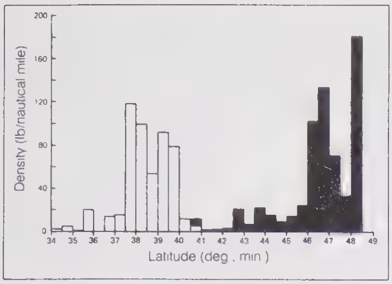

Figure 2.—Pacific ocean perch density (dark bar) and chilipepper density (clear bar) in pounds per nautical mile.

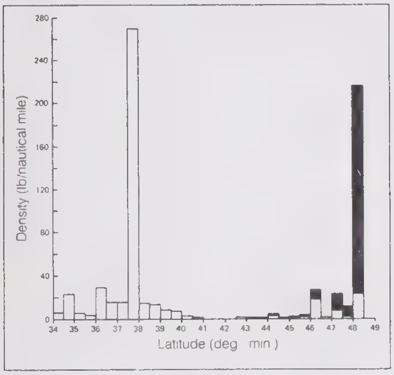

Figure 3.—Silvergray rockfish density (dark bar) and bocaccio density (clear bar) in pounds per nautical mile.

Table 4.—Binary correlation coefficients for rockfish species.

Species	Pacific ocean perch	Silvergray rockfish	Yellowtail rockfish	Chili-pepper	Shortbelly rockfish	Bocaccio	Canary rockfish
Pacific ocean perch	1.0	.057	−.052	−.316***	−.286***	−.244***	−.095**
Silvergray rockfish	—	1.0	.150***	−.109***	−.101**	.091**	.191***
Yellowtail rockfish	—	—	1.0	−.185***	−.180***	−.013	.289***
Chilipepper	—	—	—	1.0	.045	.022	−.162***
Shortbelly rockfish	—	—	—	—	1.0	.058	−.111***
Bocaccio	—	—	—	—	—	1.0	.065
Canary rockfish	—	—	—	—	—	—	1.0

* Significant at 10% level.
** Significant at 5% level.
*** Significant at 1% level.

data would have required extensive data editing. However, Figure 3 suggests an inverse relationship between abundances of these two species.

Members of the southern and northern groups of commercially important species appear as distinct entities in the correlation analysis. Members of both the northern and southern groups of species show weak positive association. Between members of the two groups, there is stong negative association.

Discussion

Among the northern and southern groups of commercially important rockfishes, several species can be paired together on the basis of similar morphologies. These species pairs also tend to be spatially segregated. This, in turn, suggests similarities in the basic adaptive strategy of these species pairs. This sort of apparent equivalence between organisms of different regions has long been noted by biogeographers (Levins, 1968).

For a rockfish species to support a commercial fishery, the species must have a large enough body size to provide a marketable fillet, be relatively abundant, and be sufficiently aggregated to provide a profitable catch per unit of effort for the fisherman. Of the approximately 70 species of rockfish off the northeastern Pacific coast, only a few rockfish species have the necessary requirements to support a commercial fishery. The fact that, within the group of commercially exploitable rockfish, certain species show strong similarity in their functional adaptive strategies, points out the importance of these particular adaptive strategies.

Acknowledgments

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AHLSTROM AND MOSER: IDENTIFICATION OF PELAGIC MARINE FISH EGGS
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CHARACTERS USEFUL IN IDENTIFICATION OF PELAGIC MARINE FISH EGGS

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ABSTRACT

Characters of importance in identifying pelagic marine fish eggs can be divided into two categories: characters independent of the embryo and characters associated with the developing embryo. Characters independent of the embryo would include egg shape, egg size, character of chorion, character of yolk, presence or absence of oil globules, and width of perivitelline space.

Planktonic marine fish eggs are usually globular in shape and range in size between 0.5 and 5.5 mm. We estimate that over 40% of the kinds of pelagic eggs are under 1.0 mm in diameter, 30% are between 1.0 and 1.5 mm, 15% are between 1.5 and 2.0 mm, and that about 14% are over 2.0 mm in diameter.

The chorion is usually smooth, but can be variously ornamented (polygonal network, spines, swellings, etc.). The perivitelline space is usually narrow but is wide in eggs of some primitive teleost groups (Anguilliformes and many clupeids). The yolk can be segmented or homogeneous. Oil globules range in number from none or one to many. About 25% of pelagic fish eggs lack an oil globule, 15% have two to many oil globules, and 60% have a single oil globule.

Characters associated with embryos would include pigment patterns, number of myomeres, length of gut, type of fin fold, position of heart, state of development at blastopore closure and at hatching, shape of yolk sac on late-stage eggs and newly hatched larvæ, position of oil globule(s) in the yolk sac, and special embryonic characters such as the elongated fin rays that form in trachipteroid eggs.

RESUMEN

Los caracteres importantes para la identificación de huevecillos de peces marinos pelágicos pueden ser divididos en dos categorías: carácteres independientes del embrión, y carácteres asociados con el embrión en desarrollo. Los carácteres independientes del embrión incluirían la forma del huevecillo, el tamaño del huevecillo, el carácter del corión, el carácter del vitelo, la presencia o ausencia de gotas oleosas, y la anchura del espacio perivitelino.

Huevecillos de peces marinos planctónicos son generalmente de forma globular y varían en tamaño entre 0.5 y 5.5 mm. Calculamos que más de 40% de los tipos de huevecillos pelágicos son menos de 1.0 mm de diámetro, el 30% son de entre 1.0 y 1.5 mm, el 15% son de entre 1.5 y 2.0 mm, y alrededor del 14% son de más de 2.0 mm de diámetro.

El corión es normalmente suave, pero puede estar distintamente ornamentado (red poligonal, espinas, inflaciones, etc.). El espacio perivitelino es normalmente estrecho, pero es ancho en los huevecillos de algunos grupos primitivos de teleósteos (anguiliformes y muchos clupéidos). El vitelo puede ser segmentado u homogéneo. Gotas oleosas varían en número desde ninguna hasta una o varias. Como 25% de los huevecillos de peces pelágicos carecen de la gota oleosa, el 15% tienen de dos a varias gotas oleosas, y el 60% tienen una sola gota oleosa.

Los carácteres asociados con embriones incluirían patrones de pigmentación, número de miómeros, longitud del intestino, tipo de pliegue de la aleta, posición del corazón, estado de desarrollo en el cierre del blastoporo y el tiempo de eclosión, la forma del saco vitelino en la última fase de los huevecillos y las larvas recién eclosionadas, la posición de la(s) gota(s) oleosa(s) en el saco vitelino, y carácteres embriónicos especiales tales como las rayas de aleta elongadas que se forman en huevecillos traquípteros.

INTRODUCTION

Oviparous marine teleosts extrude their eggs in a variety of ways. Many inshore species have demersal eggs, which are often attached to rocks, shells, or seaweed. Some build nests, and eggs are guarded by the male during incubation. Some demersal eggs are initially released in the pelagic zone, fertilized, and then sink. The chorions of these eggs are characteristically mucilaginous, permitting eggs to cling to bottom objects or to each other. Pelagic spawners usually produce separate isolated eggs, but the eggs of some species can be aggregated in various ways. They may be aggregated into large gelatinous masses or balloons (as in most scorpænid genera, and in the ophidiid genus *Brotula*) or can be spawned in gelatinous ribbon-like sheets (*Lophius antennarius*). Another method of aggregation is attachment of eggs to each other by filaments, a form of aggregation found in most exocœtoid fishes and in many atherinid fishes. In our experience except for eggs of the scomberesocid fish, *Cololabis saira*, aggregated eggs are seldom taken in plankton hauls. The number and arrangement of chorionic fila-

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[1] See memoria on page 5 of this volume. Inquiries concerning this paper may be directed to the junior author

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ments can differ strikingly among species and genera of exocœtoid fishes and provide useful characters for identification.

We are primarily interested in identifying pelagic eggs that are collected on ichthyoplankton surveys for the purpose of determining distribution and spawning biomass of target species. There are numerous contributions that describe pelagic eggs of marine fishes in order to facilitate their identification in plankton collections. The majority of such contributions are based on rearing artifically fertilized eggs from known parents or rearing mixtures of eggs collected in plankton hauls through both the embryonic and larval periods to sizes that can be positively identified. Other contributors have used the historical method of identifying eggs collected in ichthyoplankton surveys by working backwards from late-stage larvæ or juveniles that can be positively identified to earlier stage larvæ and ultimately to yolk-sac larvæ and eggs.

SUMMARY OF CHARACTERS

Plates 1 and 2

The characters of importance in identification of pelagic marine eggs are the following;

1) *egg shape*: spherical or otherwise;
2) *egg size*: pelagic marine fish eggs range in size from ca 0.5 to ca 5.5 mm;
3) *chorion*: ornamented or smooth, type of ornamentation, thickness;
4) *inner membrane*: presence or absence and location within egg;
5) *yolk*: segmented or homogeneous, nature of segmentation;
6) *perivitelline space*: width;
7) *oil globules*: number and size;
8) *embryonic characters*: state of development at blastopore closure, sequence of appearance and changes in pigmentation, pigment pattern at hatching, stage of development on late-stage embryos of various anatomical features such as eyes, mouth, fins, digestive tract, position of anus, and heart.

DESCRIPTION OF CHARACTERS

Egg Shape

Planktonic eggs are predominantly spherical, but there are some interesting exceptions. The engraulids afford the most striking exceptions; the eggs of most anchovies are ellipsoidal. The eggs of several species of engraulids approach the globular shape (*Thryssa mystax*, Delsman 1931; *Anchoa mitchilli*, Kuntz 1914; and *Setapinna phasa*, Jones and Menon 1952). Delsman (1931) described eggs of several species of *Stolephorus* that had a terminal knob at one end of the chorion. Planktonic eggs of some marine fishes in other families are not truly spherical but rather are somewhat off-round, as in the scomberesocid, *Scomberesox saurus* (Ahlstrom 1972) and in several ostraciontid species (Watson and Leis 1974; Plate 1).

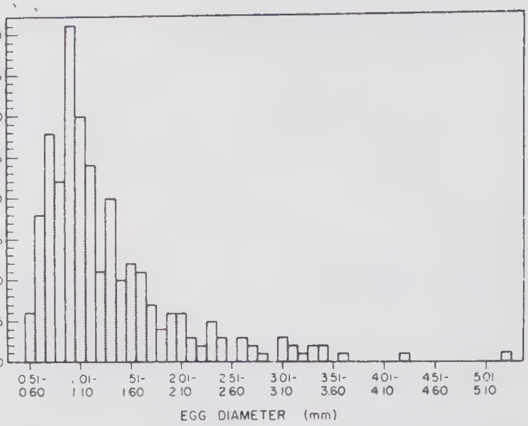


Figure 1. Frequency of egg diameter for 288 species with pelagic eggs, compiled from Mito (1961-63), Marinaro (1971), Robertson (1975), Russell (1976) and original data.

Egg Size

Pelagic fish eggs range from 0.5 mm in diameter to about 5.5 mm (Figure 1). Among the smallest marine fish eggs are those of certain bothid flatfishes and labrids, whereas the eggs of the pleuronectid flatfish, *Reinhardtius hippoglossoides* (4.0 to 4.5 mm size range), and a murænid eel from the Mediterranean (ca 5.5 mm) are the largest known. The majority of pelagic fish eggs are in the size range 0.6 to 1.6 mm. In some fishes, larger sized eggs result from the possession of a wide perivitelline space, as for example in some clupeids, most Anguilliformes, some stomiatoid fishes, and the pleuronectid flatfish genus *Hippoglossoides* (Plate 2). The yolk mass within some large eggs may be no larger than in eggs of less than 1.5-mm diameter that have a narrow perivitelline space. Some fishes that spawn larger sized eggs with the yolk mass almost filling the egg would include several pleuronectid flatfishes, most trachipteroid fishes, most exocœtoids that spawn separate pelagic eggs, various tetraodontiform fishes that spawn pelagic eggs, several argentinoid fishes, and some trichiurids and uranoscopids. This list could be made moderately extensive but, even so, would probably not include more than 10% of the kinds of pelagic marine fish eggs.

Chorion

The outermost structure of the egg is variously called the egg capsule, egg shell, vitelline membrane, egg membrane, or chorion. Although most fish eggs have smooth unornamented chorions, it can be variously and sometimes elaborately ornamented in some species. Such ornamentation can occur in several orders, including the

Salmoniformes, Myctophiformes, Gadiformes, Pleuronectiformes, Atheriniformes, Gobiesociformes, and Clupeiformes (Rass 1972). In some species where the chorion appears to be smooth and unornamented, a careful inspection, especially under higher magnification, shows the chorion to be striated or wrinkled. This is particularly true of the egg membranes of a number of pleuronectid flatfishes, which have striations or reticulations.

The ornamentation of the chorion can be limited or extensive. It can consist simply of a single protuberance or swelling, or a cluster of pustules or swellings surrounding the micropyle (Plate 1). Mito (1963b) shows several types of flatfish eggs that possess a single swelling or protuberance, and Watson and Leis (1974) illustrate an egg with a more complicated protuberance that they also assigned to a flatfish. Eggs of ostraciontids are known to have a patch of pustules on the chorion surrounding the micropyle (Watson and Leis 1974).

Of those eggs with extensive chorion ornamentation, the most widespread type consists of a honeycomb-like polygonal network formed at the outer surface of the egg membrane (Plates 1 and 2). Usually the network is hexagonal, but in some species the polygons can have 4, 5, or 7 sides intermixed with the usual 6-sided pattern. The diameters of the polygons range for example from 0.015 in *Chirocentrus dorab* (Delsman 1923) to 0.18-0.24 mm in the soleid, *Aesopia cornuta* (Mito 1963b). The pattern is well shown on scanning electronmicrographs of the pleuronectid genus *Pleuronichthys* and the synodontid genus *Synodus*, two genera that are phylogenetically remote (Sumida et al. 1979). On eggs of the macrurid genus *Coelorhynchus*, the network is removed from the chorion itself and attached to it by a series of posts (Sanzo 1933). In the distinctive egg of the sternoptychid, *Maurolicus muelleri*, the chorion is divided into a number of hexagonal facets, the junctions of which protrude as spine-like structures (Mito 1961a).

Another less common type of ornamentation on the chorion of pelagic fish eggs is spination. Spines can be relatively simple such as are found on the eggs of several exocœtids that spawn separate pelagic eggs, or they can be rather complex spine-like structures such as the ornamentation found on several types of eggs referred to the Myctophiformes (Plate 1).

Only a few of the pelagic, separate exocœtid eggs have been confidently assigned to species. Identified eggs would include eggs of two species of *Oxyporhamphus* with quite short spines distributed over the chorion and two species of *Cheilopogon*, which have fewer but somewhat longer and thinner spine-like filaments (Plate 1).

Delsman (1938) described two types of eggs that had strikingly ornamented chorions, which he referred to the Myctophoidea. The chorions are covered with short, trifid spines. On one type of egg the appendages are made up of three planes intersecting each other at an angle of 120° and ending in a point. In a second type of egg, the trifid spine-like structures end bluntly in a small hollow pit. Other eggs similar to Delsman's second type have been described from Japanese waters (Mito 1961a) and from Hawaii (Watson and Leis 1974; Plates 1 and 2).

Instead of having ornamentation on the outer surface of the chorion, eggs of fishes belonging to the salmoniform suborder Argentinoidei have pustules or swellings on the inner surface of the chorion. The pustulation can be quite marked, as in the eggs of *Microstoma* or *Nansenia*, or hardly evident, as in eggs of some bathylagid smelts.

Inner Egg Membrane

Most pelagic fish eggs lack a free inner egg membrane. The presence of an inner egg membrane occurs, for example, in eggs of some anguilliform fishes (Mito 1961a shows several example; Plate 2), in some clupeiform fishes (Delsman 1926), and in some fishes of the suborder Stomiatoidei (Sanzo 1931b; Ahlstrom and Counts 1958). The inner membrane can be quite firm, as in eggs of *Chauliodus sloani* (Mito 1961a), or it can be thin and irregular in outline, as in eggs of *Vinciguerra lucetia* (Ahlstrom and Counts 1958). In the latter, the inner membrane lies close to the chorion. In the egg of *Chauliodus sloani*, which has a wide perivitelline space, the inner membrane is much closer to the embryo, and in the egg of *Argyropelicus hemigymnus* it adheres in places to the yolk (Sanzo 1931b).

Yolk

The yolk mass dominates the newly spawned fish egg and is usually translucent and unpigmented. The yolk is segmented in eggs of most "primitive" teleosts but is homogeneous in the majority of eggs of "higher" teleosts (Plates 1 and 2). Segmented yolk is found in some of the latter group (principally among the perciforms and pleuronectiforms) at the end of the embryonic period. In addition to the character of segmented versus homogeneous yolk, the shape of the yolk sac, particularly in late-stage eggs or new-hatched larvæ, is a useful character. Also the presence of pigmentation and its characteristic distribution may help in identification.

Segmentation of the yolk can range from coarse to fine. Delsman found the type of segmentation to be an important character for distinguishing the eggs of clupeoids. He found the yolk to be finely segmented in eggs of *Dussumieria hasseltii* (Delsman 1925), moderately fine in eggs of most species of *Ilisha* (Delsman 1932), and coarsely segmented in eggs of *Anodontostoma chacunda* (Delsman 1926).

Segmentation of the yolk among eggs of a given species can be quite variable. Ahlstrom and Counts (1958) commented on the variability observed in eggs of the stomiatoid *Vinciguerria lucetia*, especially noticeable in early-stage eggs. The yolk in some eggs was nearly homogeneous, in others partly segmented, and in still others completely segmented into globules.

In some "higher" teleosts the segmentation is confined to the periphery of the yolk, as in eggs of various soleids (see Russell 1976). In others, for example the carangid, *Trachurus symmetricus*, where segmentation becomes rather complete, it can progress from little or no segmentation in newly spawned eggs to rather complete segmentation in late-stage eggs (Ahlstrom and Ball 1954).

Explanation of Plates

Captions under each plate indicate the species and the diameter or dimensions of the egg in mm.

Plate 1

Uranoscopus scaber, from Dekhnik (1973).
Pleuronichthys cornutus, from Mito (1963b).
Leuroglossus stilbius, from Ahlstrom (1969).
Cheilopogon nigricans, from Parin and Gorbunova (1964).
Maurolicus muelleri, from Mito (1961a).
Aesopia cornuta, from Mito (1963b).
Cheilopogon katoptron, from Kovalevskaya (1965).
Myctophiform, from Watson and Leis (1974).
Pleuronectiform, from Watson and Leis (1974).
Oxyporhamphus meristocystis, from Parin and Gorbunova (1964).
Ceratacanthus cirrus, from Sanzo (1939).
Ostraciontid, from Watson and Leis (1974).

TYPES OF ORNAMENTATION ON CHORIONS OF PELAGIC MARINE FISH EGGS

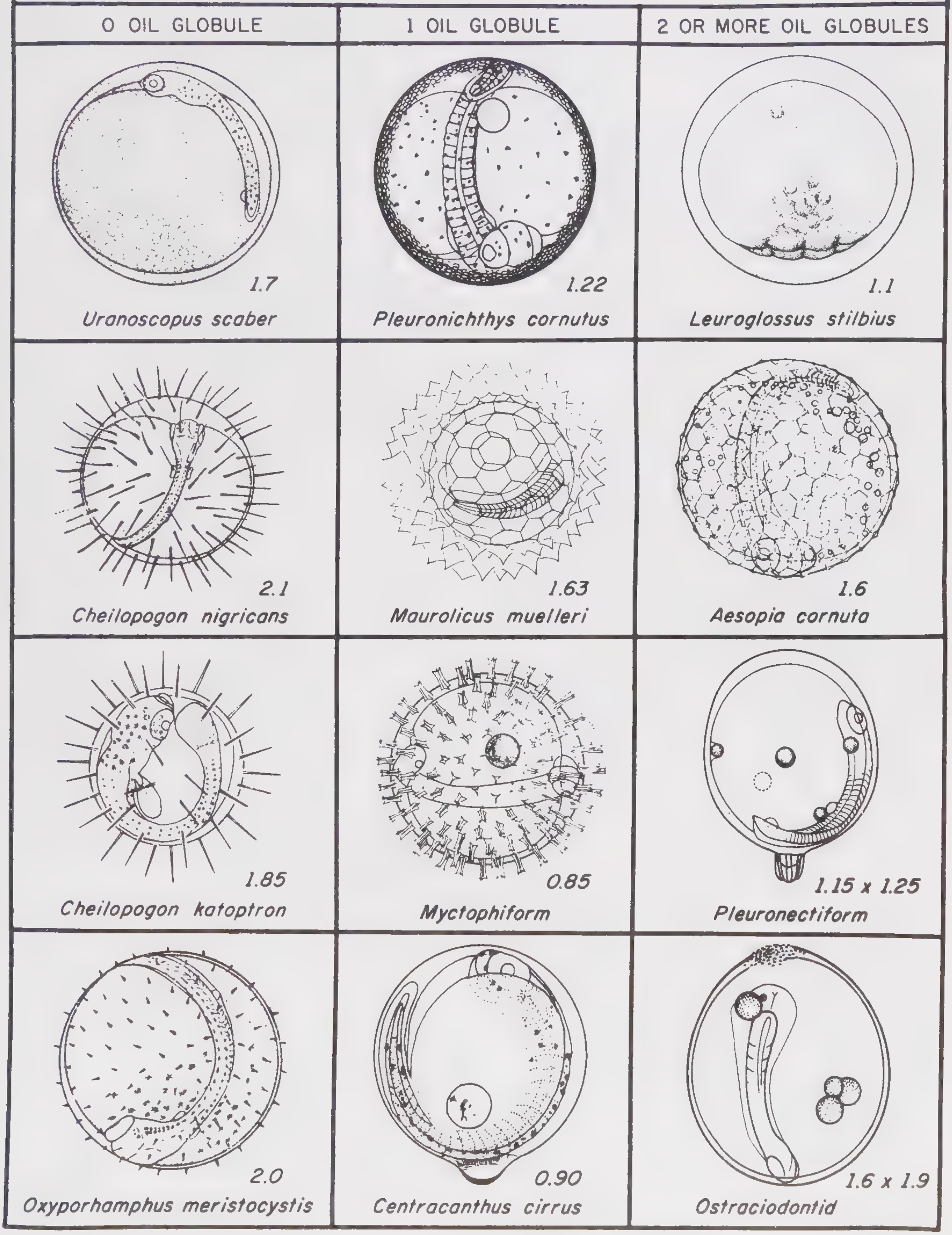
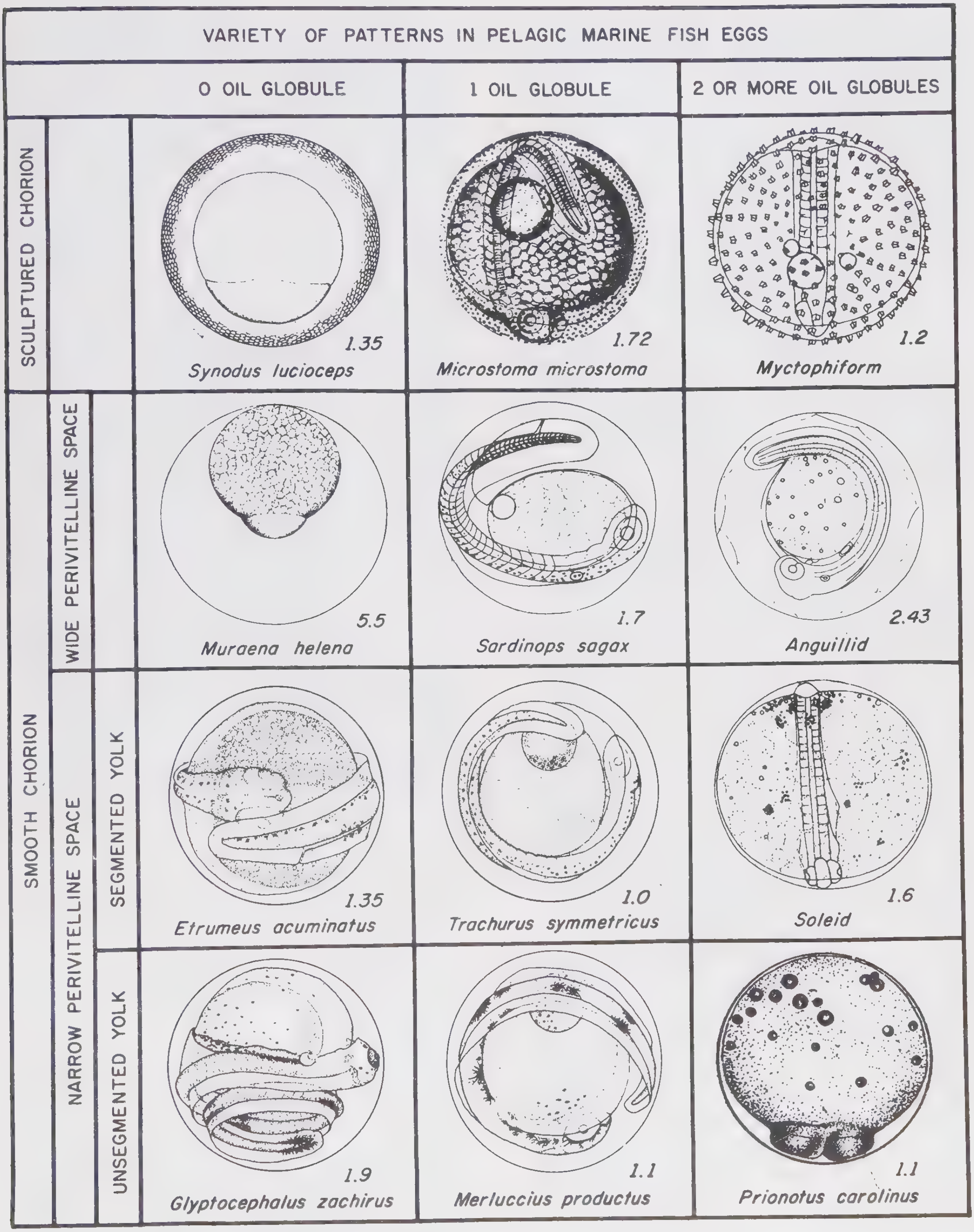

0 OIL GLOBULE
1 OIL GLOBULE
2 OR MORE OIL GLOBULES
1.7
Uranoscopus scaber
1.22
Pleuronichthys cornutus
1.1
Leuroglossus stilbius
2.1
Cheilopogon nigricans
1.63
Maurolicus muelleri
1.6
Aesopia cornuta
1.85
Cheilopogon katoptron
0.85
Myctophiform
1.15 x 1.25
Pleuronectiform
2.0
Oxyporhamphus meristocystis
0.90
Centracanthus cirrus
1.6 x 1.9
Ostraciodontid

Plate 2

Synodus lucioceps, original.
Microstoma microstoma, from Sanzo (1931a).
Myctophiform, from Mito (1961a).
Muraena helena, from Grassi (1913).
Sardinops sagax, from Mito (1961a).
Anguillid, from Mito (1961a).
Etrumeus acuminatus, original.
Trachurus symmetricus, from Ahlstrom and Ball (1954).
Soleid, from Mito (1963b).
Glyptocephalus zachirus, original.
Merluccius productus, from Ahlstrom and Counts (1955).
Prionotus carolinus, from Kuntz and Radcliffe (1917).


VARIETY OF PATTERNS IN PELAGIC MARINE FISH EGGS
0 OIL GLOBULE
1 OIL GLOBULE
2 OR MORE OIL GLOBULES
SCULPTURED CHORION
1.35
Synodus lucioceps
1.72
Microstoma microstoma
1.2
Myctophiform
SMOOTH CHORION
WIDE PERIVITELLINE SPACE
5.5
Muraena helena
1.7
Sardinops sagax
2.43
Anguillid
NARROW PERIVITELLINE SPACE
SEGMENTED YOLK
1.35
Etrumeus acuminatus
1.0
Trachurus symmetricus
1.6
Soleid
UNSEGMENTED YOLK
1.9
Glyptocephalus zachirus
1.1
Merluccius productus
1.1
Prionotus carolinus

Perivitelline Space

In the majority of pelagic fish eggs the perivitelline space is narrow; however, eggs with a wide perivitelline space are the basic type among eels, are common among clupeiform fishes, and are encountered in stomiatoid fishes (Plate 2). All of these examples are "primitive" teleosts whose eggs have regularly segmented yolk. Fishes with homogeneous yolk seldom have a wide perivitelline space. A well-known exception is the flatfish genus *Hippoglossoides*, whose several species have pelagic eggs with a wide perivitelline space (Pertseva-Ostroumova 1955). The eggs of the striped bass, *Morone saxatilis*, also have a wide perivitelline space; however, this species enters estuaries or rivers to spawn, and the eggs are semibuoyant.

When first spawned, even those pelagic fish eggs that ultimately develop a wide perivitelline space have little or no perivitelline space. In the Pacific sardine, *Sardinops caeruleus*, Miller (1952) found that the perivitelline space was small or nonexistant at time of extrusion from the female. The perivitelline space was almost completely formed within 2 hours after fertilization as a result of hydration. Egg diameter increased from 1.15 mm at fertilization to 1.64 mm after 2 hours, to the maximum diameter of 1.83 mm at 10 hours after fertilization. Since a fully formed perivitelline space requires some time to develop, its absence in recently spawned eggs can be misleading. In species that will ultimately develop a wide perivitelline space, it is helpful to give the diameter before and after hydration. Also in eggs with a wide perivitelline space, the diameter of the yolk mass is a useful measurement.

Oil Globule

For identifying pelagic marine fish eggs, perhaps no character is more important than the number of oil globules. Examples of species that lack oil globules in their yolk are known for many teleost orders, although for some of the orders, known examples are limited to one or a few species. Major families in which the eggs of all or many species lack an oil globule would include the Engraulidæ, Synodontidæ, Gadidæ,and Pleuronectidæ. Two other commonly occurring groups whose eggs lack an oil globule are the Trachipteroidei and Exocœtoidei.

Examples of pelagic eggs with multiple oil globules are known for at least seven orders. Multiple oil globules occur most frequently in anguilliform eels, bathylagid smelts, soleid and cynoglossid flatfishes, and in tetraodontiform fishes. The number of multiple oil globules can range from few (less than 10) to many (more than 50). The largest numbers occur in eggs of some soleid flatfishes. When numerous, oil globules tend to aggregate into clusters, and the pattern of distribution of the oil globules within the yolk mass can be useful in egg identification. In bathylagid smelts, the oil globules undergo remarkable migrations during embryonic development (Ahlstrom 1969).

The most common kind of pelagic fish egg is that with a single oil globule. This is true, for example, in most perciform families, in several families of flatfishes, and in many gadoids, stomiatoids, and clupeoids. A compilation of data from Mito (1961-63), Marinaro (1971), Robertson (1975), Russell (1976), and our California Cooperative Oceanic Fisheries Investigations (CalCOFI) area shows that for a total of 515 species, 24.5% lacked an oil globule, 60.1% had one oil globule, and 15.3% had multiple oil globules (Table 1). In eggs with a single oil globule, it usually lies at the vegetal pole opposite to the blastodisc and developing embryo. The single oil globules can range in size from < 0.10 mm to > 1.0 mm. The oil globule in formaldehyde-preserved pelagic eggs is usually colorless or faintly yellowish or reddish.

In eggs having a single oil globule, the position of the oil globule in the yolk sac can be of diagnostic value. The usual position of the oil globule is in the rear of the yolk sac; however, in a moderate number of families it is far forward in the yolk sac, as for example in labrids, most carangids, mullids, and lethrinids. In some genera the position of the oil globule can vary from species to species. Thus, two species of *Sphyraena* have the oil globule in a forward position (*S. pinguis* in Shojima et al. 1957; *S. borealis* in Houde 1972), and two species of *Sphyraena* have the oil globule in the rear of the yolk sac. (*S. sphyraena* in Vialli 1956; *S. argentea* in Orton 1955). In some species the oil globule is in an intermediate position or slightly forward. Several examples drawn from three families are serranids such as *Serranus cabrilla* (Raffaele 1888) and *Lateolabrax japonicus* (Mito 1963a); clupeids such as *Konosirus punctatus* (Uchida et al. 1958), *Harengula pensacolae* (Gorbunova and Zvyagina 1975) and *Brevoortia smithi* (Houde and Swanson 1975); and argentinids such as *Argentina silus* (Schmidt 1906) and *Nansenia oblita* (Sanzo 1931a).

Embryonic Characters

We have found it helpful to divide embryonic development in the egg into three stages: early (fertilization to blastopore closure), middle (from blastopore closure to the time that the separating tail begins to curve laterally away from the embryonic axis), and late (from the time that the tail is curved away from the embryonic axis to the time of hatching).

In eggs of some fishes the embryo is undergoing organogenesis prior to blastopore closure, whereas in others the embryo is relatively undifferentiated at closure of the blastopore. For example, in the Pacific hake, *Merluccius productus*, when the embryonic shield has enveloped approximately three-fourths of the yolk, the embryo has a discernible eye. Just before blastopore closure, 10 to 13 myomeres are visible behind the head of the developing embryo (Ahlstrom and Counts 1955). Similarly, in the jack mackerel, *Trachurus symmetricus*, the myomeres

TABLE 1

Frequency of Character Combinations in Pelagic Marine Fish Eggs.

	Oil Globules						All categories	
	0		1		2 or more			
	No.	%	No.	%	No.	%	No.	%
Ornamented chorion	23	4.5	18	3.5	11	2.1	52	10.1
Chorion smooth								
Wide perivitelline space	15	2.9	12	2.3	17	3.3	44	8.5
Segmented yolk, narrow perivitelline space	15	2.9	62	12.0	11	2.1	88	17.0
Homogeneous yolk, narrow perivitelline space	73	14.2	218	42.3	40	7.8	331	64.3
Total all categories	126	24.5	310	60.1	79	15.3	515	99.9

appear behind the head and the optic vesicles form shortly before blastopore closure (Ahlstrom and Ball 1954). In contrast, in argentinoid smelts the embryo is a simple undifferentiated ridge at blastopore closure.

In late-stage eggs a suite of characters can be used, including the shape of the developing embryo, its myomere count, the position of the anus on the body, and the nature of the finfold. Pigmentation usually begins forming on middle-stage eggs and reaches its fullest development on later stage eggs. In many kinds of eggs there is a sequence of changes in pigmentation during embryonic development. The pigment pattern may be confined to the embryo itself, or it can be developed over part or all of the yolk sac and may extend out into the finfolds. Also, it may be variously developed in relation to the oil globule if present. The melanophores originate from the neural crest region and usually first appear along the dorsal and dorso-lateral surfaces of the embryo. In many species the embryonic pigment at hatching is aligned along the dorsal margins of the body, often extending from the head to the end of the notochord.

For the majority of marine fishes with pelagic eggs, the yolk-sac stage is a period of rearrangement (migration) of melanophores from the predominant dorsal position on newly hatched larvæ to their predominantly ventral position on late yolk-sac larvæ. Some species, however, begin or even complete the migration and rearrangement of body melanophores before hatching. The mackerel, *Scomber japonicus*, furnishes an example where the downward movement of the dorso-lateral row of melanophores commences on late-stage embryos (Kramer 1960). Examples of species that reach a more advanced, although still intermediate, phase of rearrangement of melanophores on late-stage embryos are bonito, *Sarda lineolata* (Orton 1953); Pacific hake, *Merluccius productus* (Ahlstrom and Counts 1955); and cod, *Gadus morhua* (Fridgeirsson 1978). Several groups of fishes complete the rearrangement of pigment in the late-stage pelagic eggs, and the pattern is similar to that found in yolk-sac larvæ and on into the preflexion larval stage. A few examples are the carangid, *Seriola quinqueradiata* (Mito 1961b); stromateoids from several families (Ahlstrom et al. 1976); *Trachipterus* sp. (Mito 1961b); and the cynoglossid, *Areliscus trigrammus* (Fujita and Takita (1965). A variant of this is found in species that develop heavy pigment over the head and body of their embryos and retain such heavy pigmentation during the yolk-sac stage and larval period. Various flatfishes develop heavily pigmented embryos as, for example, in all species of *Pleuronichthys* (Sumida et al. 1979), in *Hypsopsetta* (Eldridge 1975), in *Scophthalmus rhombus* (Ehrenbaum 1905-1909), and in *Verasper variagatus* (Mito 1963b). Examples from other groups are *Coryphaena hippurus* (Mito 1961b), *Cololabis saira* (Hatanaka 1956), *Zeus faber* (Dehknik 1973), and *Mugil auratus* (Dehknik 1973).

Some pelagic eggs lack melanophores on late-stage embryos or at best have a few inconspicuous melanophores. Embryos and newly hatched larvæ of engraulids lack melanophores. When melanophores become visible later in the yolk-sac stage, they already are ventral in position, lying along the gut and on the ventral margin of the tail. It is assumed that the pigment cells in Engraulidæ migrate as in the Clupeidæ but pigment formation is delayed until cells have reached more or less permanent locations. Other examples of fishes with this type of melanophore migration are two species of *Girella* (Orton 1953; Uchida et al. 1958); the Pacific halibut, *Hippoglossus stenolepis* (Thompson and Van Cleve 1936; Pertseva-Ostroumova 1961); the argentinid, *Argentina silus* (Schmidt 1906), and several synodontids (Mito 1961a).

Although larvæ of some groups develop specialized larval characters such as elongated fin rays and head spination, such characters are seldom developed on embryos. A striking exception is the development of elongated elaborate dorsal and pelvic fin rays in embryos of trachipteroids. Another such character is the pair of appendages that develop during the embryonic period on the head of *Champsodon* spp. (Mito 1960, 1962).

The size and state of development at hatching is related to egg diameter for eggs with a narrow perivitelline space and to yolk size for those with a wide perivitelline space. The length of a larva at hatching is usually 2.5-3.0 times the diameter of the egg. Larvæ hatching from small eggs are usually underdeveloped in that they lack a functional mouth, pigment in the eyes, and fins of any sort. Other organs are similarly underdeveloped. Larvæ hatching from large eggs usually are much better developed. The eyes can be pigmented, the mouth formed, and the larval pectoral fins developed. In eggs of flying fishes, flexion of the caudal fin precedes hatching, and in some species of the group the other fins are well developed before hatching. An interesting exception to the correlation of large egg size and advanced development before hatching is found in *Argentina silus* (Schmidt 1906). This species has a large egg (ca 3.0-3.5 mm), an enormous oil globule (0.95-1.18 mm), and lacks a perivitelline space in early-stage eggs. At hatching, the yolk-sac larva of *S. silus* is as underdeveloped as in those species that hatch from eggs in the 0.6-1.0-mm size range. The eyes are unpigmented, the mouth undeveloped, and the pectoral fins lacking.

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SURVIVAL AND MORTALITY IN A POPULATION OF ADÉLIE PENGUINS[1]

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Abstract. Life table and survivorship estimates were calculated for Adélie Penguins (*Pygoscelis adeliae*) of known age, sex, and breeding status. Fledglings had been banded and web-punched in nine consecutive breeding seasons at Cape Crozier, Ross Island. During four later seasons the returns of 2- to 14-yr-olds were recorded. Adjustments for band loss and emigration were made in the data. Survivorship estimates were also calculated for the Yellow-eyed Penguin (*Megadyptes antipodes*) using Richdale's (1949, 1957) data. Results indicate that breeding is risky, especially in the Adélie Penguin and particularly among younger breeders. In both species, females breed at younger ages than males and in any mature age class a greater proportion of females than males breed. These factors result in higher mortality among females and a sex ratio that changes to favor males in the older age groups. The oldest individuals tend to be those that are habitually inept breeders or nonbreeders. The higher annual mortality and shorter life-span in the Adélie Penguin compared to the Yellow-eyed Penguin are probably due in part to heavier predation pressure.

Key words: Adélie Penguin; annual survivorship; Antarctica; life table; New Zealand; predation; sex ratios; Yellow-eyed Penguin.

INTRODUCTION

Among higher vertebrates penguins are relatively easy to census, capture, mark, and observe. Not surprisingly, one of the earliest avian population studies of a long-lived species was conducted on the Yellow-eyed Penguin (*Megadyptes antipodes*), by Richdale (1949, 1957) at the Otago Peninsula, New Zealand. In the present paper aspects of Adélie Penguin (*Pygoscelis adeliae*) population biology are presented and contrasted with the Yellow-eyed Penguin. Data for the latter species come entirely from Richdale's work, although life table calculations are our responsibility.

These two species are similar in that they breed annually, mated adults produce a maximum of two fledglings per breeding attempt, and they are similar in body size. They differ in that the Adélie seems to lead a more rigorous life. It is a highly migratory, diurnally active, open-nesting, and colonial penguin of high latitudes whereas the Yellow-eyed is a sedentary, nocturnally active (on land), burrow-nesting and noncolonial penguin of much lower, milder latitudes. Adélies raise their young during a 3-mo period but Yellow-eyed Penguins do so in 5.5 mo.

METHODS

The Adélie Penguin was studied at Cape Crozier, Ross Island, Antarctica (77°31′S, 169°23′E), site of a large breeding population (Fig. 1). Approximately 173 000 breeding adults were present in the Crozier West Rookery, and no detectable change in population size was noted during the period of this study (Oelke 1975, Butler and Müller-Schwarze 1977).

Each year from 1962 to 1970, Johns Hopkins University personnel banded 2000–5000 chicks just before fledging. Numbers on the aluminum wing bands were large enough to be read with 8 × 30 binoculars from a distance of 10 m. In 1964 the band design was improved; penguins having the old-style band, as described in Sladen and Penney (1960), were caught in a hand net and their band was exchanged for a new one, as described in Sladen and LeResche (1970). In subsequent years if any bands showed signs of opening, their owners were caught and the band was readjusted. In many cases this could be accomplished by placing one hand over a bird's eyes (to quiet it) while it incubated eggs and with the other hand adjusting or closing the band.

As a check against band loss, tiny holes were punched into the webs of a chick's feet using a leather punch. The number and location of punch holes (outer vs. inner web; right vs. left foot) were different for each year of banding. During November and January population peaks in the 1968–69, 1969–70, 1974–75, and 1975–76 austral summers, surveys were conducted to look for birds that had lost their bands. All colonies (groups of contiguous territories: Penney 1968) in study areas B, C, and part of N (Fig. 1) were circled

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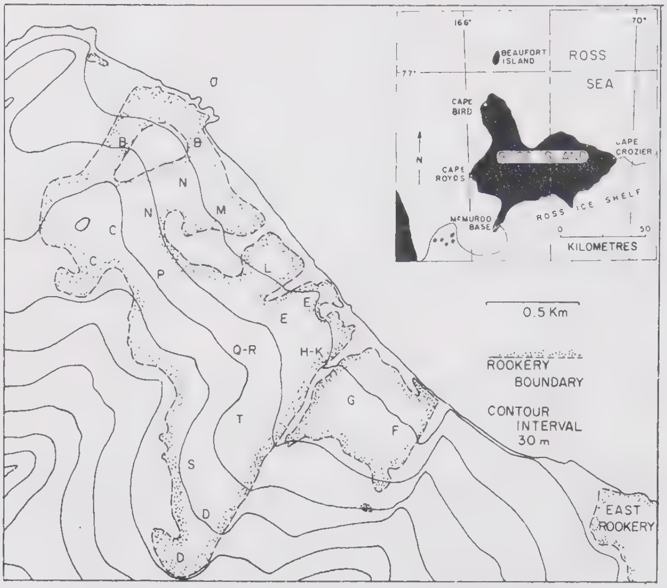

FIG. 1. The study areas designated by letters, set up by the United States Antarctic Research Program (USARP) Bird Banding Program at Crozier's West Rookery, and (insert) the location of Cape Crozier relative to other rookeries in the southern Ross Sea.

while the observer looked only at penguin feet. When a web-punched foot was sighted, the observer then looked to see if the bird was banded. If it had no band, it was caught and rebanded.

Only sightings of banded birds during the 1968–69, 1969–70, 1974–75, and 1975–76 field seasons were included in this analysis because surveys for banded penguins were known to be as complete as humanly possible during those seasons (Table 1). Furthermore, only birds banded in study areas B and C (two of four areas at Crozier where chicks were banded) were included in analyses because the western third of Crozier's West Rookery (where B and C are located) was most easily accessible and most intensively studied. Since Adélies tend to breed very near to their natal colonies (LeResche and Sladen 1970), it is most likely that if a bird from one of these two areas was not found it was not present. To be sure, the middle third of the rookery (includes banding area E) was searched almost as thoroughly, i.e., virtually every day. The eastern third of the West Rookery (includes banding area D) and the East Rookery were searched for banded birds each year during the occupation and reoccupation periods (cf. Sladen 1958) when seasonal peaks in the population occur. Data for birds 2–4 yr of age were gathered during the 1968–69 and 1969–70 seasons. Data for 5- to 14-yr-olds were gathered during the 1974–75 and 1975–76 seasons. Dates for data gathering at Cape Crozier were as follows: 24 October 1968–17 January 1969, 21 October 1969–5 February 1970, 19 October 1974–26 January 1975, and 20 October–17 December 1975.

RESULTS

Adjustments for band loss, emigration and comparability of years

The results of web-punch surveys to detect band loss are shown in Table 2, where the proportion of birds having lost bands in each cohort was compared to the age of the band in years. Because in some years a number of chicks was web-punched but not banded, we had to determine the percentage decrease in the proportion of birds having bands in subsequent years. Using the resultant fitted curve for band loss, recoveries as shown in Table 2 were adjusted in each age group by the formula:

$$z = \frac{x}{1 - y},$$

where x = number of bands recovered, y = proportion of bands lost, and z = number of bands recovered if there had been no loss. Recoveries adjusted for band loss are summarized in Table 3. For cohorts originally banded with the old-style band, recoveries in later years were adjusted using the formula shown in the footnote of Table 3. We had to assume that band loss for both band styles was equal, although it is likely that loss was slightly higher for the old style; we also assumed that all birds were rebanded at age 3 yr. A

Table 1. Band recovery data from 1968–69, 1969–70, 1974–75, and 1975–76.

Year banded	Number banded	Age of recovery (yr)												
		2	3	4	5	6	7	8	9	10	11	12	13	14
1961–62	2308						34	27					5	4
1962–63	4110					104	95					31	22	
1963–64	4998				216	172					73	41		
1964–65	3080			264	181					83	34			
1965–66	3800		320	258					72	40				
1966–67	3600	355	279					113	71					
1967–68	4000	428					301	192						
1968–69	2950					363	216							
1969–70	2322				301	197								

small proportion was in fact rebanded at ages 2, 4, and 5 yr.

Besides band loss, emigration can also result in the apparent disappearance of a bird from a population. Fortunately, two of the four other Adélie rookeries (Penney 1968) in the southern Ross Sea were visited by ornithologists searching for banded birds for extended periods almost yearly through 1971, and the other two were visited intermittently. Thus we have approximate emigration rates for this population. Fig. 2 compares the number of banded Crozier birds at four other rookeries and relates these numbers to the distance from the Cape Crozier West Rookery. These other rookeries and their distances were: Crozier East Rookery, 2 km; Cape Bird and Beaufort Island, each 61 km; and Cape Royds, 100 km (Fig. 1). Only birds 5 yr of age and older, through 1971, were used in Fig. 2 because many younger birds characteristically wander from rookery to rookery but then eventually return to their natal rookeries for breeding. Given that appreciable movement was detected in only 51 birds out of 18 296 banded (0.28%, $\sigma < 0.01$), emigration does not appear to be a major factor in the Crozier population. Even so, the emigrants were included in Table 1 and in further analyses.

Table 2. Estimation of band loss as a function of band age. Based on surveys conducted in 1968–69, 1969–70, 1974–75, and 1975–76.

Band age (yr)	Birds inspected (n)	Proportion currently banded	Proportion originally banded and web-punched*	Observed band loss (%)	Fitted band loss† (%)
2	15	1.00	1.00	0.0	1.0
3	45	0.97	0.99	2.0	1.3
4	31	0.87	0.89	2.0	1.7
5	51	1.00	1.00	0.0	2.2
6	89	0.99	1.00	1.0	2.9
7	66	1.00	1.00	0.0	3.8
8	16	1.00	1.00	0.0	4.9
9	13	0.92	0.99	7.1	6.4
10	23	0.74	0.84	11.9	8.4
11	…	…	…	…	11.1

* Some birds were only web-punched in some years.

† Curve fitted to exponential equation: $y = 0.574e^{0.269x}$, where y = band loss and x = age of band in years.

Two sets of years were used in order that as many age groups as possible were represented in analyses, 1968–69 to 1969–70 for 2- to 4-yr-olds and 1974–75 to 1975–76 for 5- to 14-yr-olds. Mortality during the two sets of seasons did, however, appear to differ slightly as shown by comparing three age groups, 5-, 6-, and 7-yr-olds, that occurred in both sets of years (Table 4). Lumped survivorship of these ages was 83% (σ = 0.04) from 1968–69 to 1969–70 and 63% (σ = 0.02) from 1974–75 to 1975–76 (Table 4). The difference is statistically significant (adjusted $\chi^2 = 32.02$, $P < .01$, df = 1; Steel and Torrie 1960: 371). It is possible that the 63% survivorship is a conservative estimate. Some

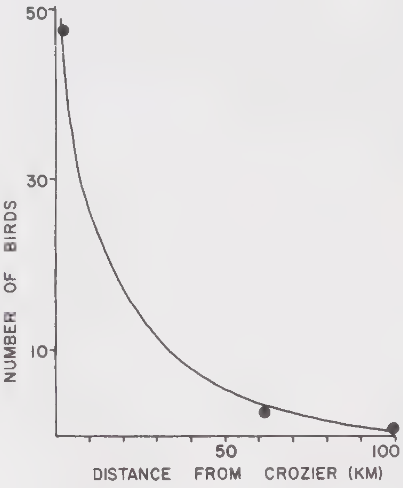

Fig. 2. The number of 5-yr or older Adélies banded at the Cape Crozier West Rookery and subsequently sighted at other rookeries in the southern Ross Sea compared to the distances between these and Crozier's West Rookery; data were combined for Cape Bird and Beaufort Island because they were equidistant from Crozier. The curve is described by the equation, $y = 44.4e^{-0.039x}$.

TABLE 3. Band recovery data adjusted for band loss. Recovery data from Table 1; correction data from Table 2.

Year banded	Number banded	Age of recovery (yr) 2	3	4	5	6	7	8	9	10	11	12	13	14
1961–62	2308						35*	28*					6*	5*
1962–63	4110					107*	98*					34*	24*	
1963–64	4998				221*	177*					78*	44*		
1964–65	3080			269	185					91	38			
1965–66	3800		324	262					77	44				
1966–67	3600	359	283					119	76					
1967–68	4000	432					313	202						
1968–69	2950					374	225							
1969–70	2322				308	203								

* All birds originally banded before the 1964–65 season were rebanded as 3-yr-olds. Therefore, band loss was adjusted for with the equation: estimated band loss (%) = $1.3 + 0.574e^{0.269(x-3)}$, where x = age of the bird or band in years (see Table 2, second footnote).

additional 5-yr-olds, and perhaps 6-yr-olds, but not older individuals may have arrived after our departure in mid-December 1975. This is because younger Adélie Penguins tend to arrive later at the rookery than older ones (LeResche 1971, Ainley 1975). On the other hand, there may have been real differences in mortality related to environmental conditions. Ainley and LeResche (1973) showed that pack ice conditions could have major effects on the breeding biology and productivity of Adélies. Environmental conditions might also have affected mortality enough that there would be notable differences between years, as observed for Yellow-eyed Penguins by Richdale (1957). For instance, the unusually heavy and persistent pack ice in the 1968–69 season delayed Adélie migration to Crozier and led to a low proportion of breeding birds (Ainley and LeResche 1973). Since mortality is so high in breeders (see below), being prevented from breeding might have resulted in increased survival of birds to the 1969–70 season. Additional census seasons may have allowed us to correct for this. In any case, it should be noted that the annual survivorship for 1974–75 to 1975–76 may be slightly low or for 1968–69 to 1969–70 slightly high, one group relative to the other.

Life table and survivorship estimates

Partial horizontal life tables were constructed (Tables 5, 6, and 7) using the data in Table 3. These are only partial life table analyses because data on age-specific fecundity are yet to be analyzed; it will be some time before they are available. Curves generated from the resultant survivorships are all monotonic as expected. The difference in survivorship (l_x) between the two sets of years is quite evident ($\chi^2 = 777$, $P < .05$, df = 3).

This difference suggests that the mortality of chicks or yearling birds was greater between 1961–62 and 1964–65 than it was between 1966–67 and 1969–70. It is interesting that annual survivorship values (Table 4) for these two sets of data are opposite in pattern to the l_x values. The fact that when l_x estimates are relatively low, annual survivorship estimates are relatively high, may reflect some sort of compensatory mortality. Another possibility is that band loss was greater during the first 3 yr of study when the old-style band was employed. Our correction factor, based on loss rates of the new-style band (Table 3, footnote), was perhaps not fully adequate. More information is needed to assess these premises.

The data on 5- to 14-yr-olds in Table 7 were used to generate a survivorship curve for Adélies (Fig. 3). When the same curve was extended to younger ages, data points diverged radically from it, due to the fact that many Adélies 4 yr of age and younger, and occasionally 5-yr-olds, had not yet returned to the rookery since fledging; by 6 yr, all Adélies that are going to return to their natal rookery have done so for the first time. Because of this it was not possible to generate survivorship curves for younger birds. Also presented in Fig. 3 is a survivorship curve for Yellow-eyed Penguins based on Ricklefs' (1973) survivorship

TABLE 4. Comparison of annual survivorship from year 1968–69 to 1969–70 with that from 1974–75 to 1975–76.

	1968–69 to 1969–70			1974–75 to 1975–76		
Age, year i	Number, year i	Number, year $i+1$	Annual survival	Number, year i	Number, year $i+1$	Annual survival
2	359	283	0.788			
3	324	262	0.809			
4	269	185	0.688			
5	221	177	0.801	308	203	0.659
6	107	98	0.916	374	224	0.599
7	35	28	0.800	313	202	0.645
8				119	76	0.639
9				77	44	0.571
10				91	38	0.418
11				78	44	0.564
12				34	24	0.706
13				6	5	0.833
T	1315	1033	0.786	1400	860	0.614

TABLE 5. Comparison of l_x values from 1968–69 to 1969–70 data with data from 1974–75 to 1975–76.

	1968–69 and 1969–70			1974–75 and 1975–76			
Age x	Number banded as chicks	Number recovered at age x	l_x	Number banded as chicks	Number recovered at age x	l_x	Ratio of increase
5	8078	406	0.050	2322	308	0.133	1.66
6	9108	284	0.031	5272	577	0.109	2.51
7	6418	133	0.021	6950	538	0.077	2.67
8	2308	28	0.012	7600	321	0.042	2.50

analysis of Richdale's (1957) data. We corrected Ricklefs' values to allow for the fact that the population increased by 230% during the study (Table 8). Richdale, in fact, attributed the increase to enhanced survival of adults. Comparison of survivorship curves indicated that Yellow-eyed Penguins live longer than Adélies. Only 0.2% of banded Adélies survived 14 yr. The oldest was estimated to be 16 yr. That bird was banded as an adult of unknown age but its behavior suggested that it was 4 or, perhaps, 5 yr old when banded. It would appear from the curve that 16 yr would be near the maximum age for Adélie Penguins. Richdale (1957) had known-age individuals of 17 yr, and some unknown individuals estimated to be ≈19 yr. The curve confirms his suggestion that the oldest Yellow-eyed would live for ≈22 yr or perhaps slightly longer.

The lumped annual survivorship of 1400 Adélies 5–13 yr old from 1974–75 to 1975–76 was 61.4% ($\sigma = 0.01$) based on the values presented in Table 4. Average annual survivorship based on the curve (survivors/100 birds originally banded) was 69.6% ($\sigma = 0.17$), which is fairly close to the other estimate. The lumped annual survivorship of 630 Yellow-eyed Penguins 5–13 yr old was 86.2% ($\sigma = 0.02$), as calculated from Richdale (1957: Table 69). Average annual survivorship based on the curve for the same Yellow-eyed Penguin age classes as calculated by Ricklefs but corrected for an increasing population (Table 8), was 87.2% ($\sigma = 0.02$). Annual survivorship is much lower in adult Adélies than in adult Yellow-eyed Penguins.

Factors affecting survivorship

It was possible to determine whether survivorship was related to age. The lumped annual survivorship of 61.4% was multiplied by the (corrected) number of birds observed in each age group during 1974 (column 5 of Table 4) to derive expected values. These were compared in a χ^2 test with those observed alive in 1975. For birds 6–13 yr old, annual survival was independent of age ($\chi^2 = 6.58$, $P > .05$, df = 6). This, however, was not true when breeding status and younger birds were considered (see below).

When Adélies were grouped by age, sex, and breeding status, interesting differences in annual mortality became obvious. To establish a sufficient sample among older individuals, birds 11 yr and older were combined into one group (Table 9). From these mor-

TABLE 6. Partial horizontal life table for the Adélie Penguin. Data from Table 3.

	l_x Year banded as chick								
Age (yr)	1961–62	1962–63	1963–64	1964–65	1965–66	1966–67	1967–68	1968–69	1969–70
0									
1									
2						0.100	0.108		
3					0.085	0.079			
4				0.087	0.069				
5			0.044	0.060					0.133
6		0.026	0.035					0.123	0.087
7	0.015	0.024					0.078	0.076	
8	0.012					0.033	0.051		
9					0.020	0.021			
10				0.030	0.012				
11			0.016	0.012					
12		0.008	0.009						
13	0.003	0.006							
14	0.002								

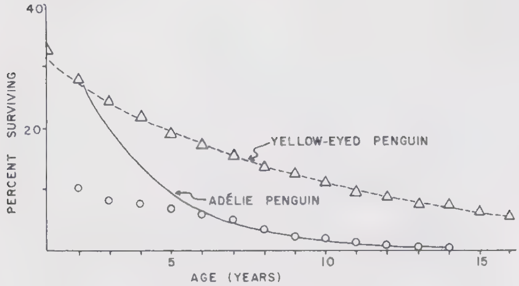

FIG. 3. A comparison of survivorship curves for Yellow-eyed Penguins at Otago Peninsula, New Zealand, during 1934–1952 and for Adélie Penguins at Cape Crozier during 1962–1976. The data points, for ages 5 yr and older, from Tables 7 and 8, were used to generate the curves, fitted by least squares.

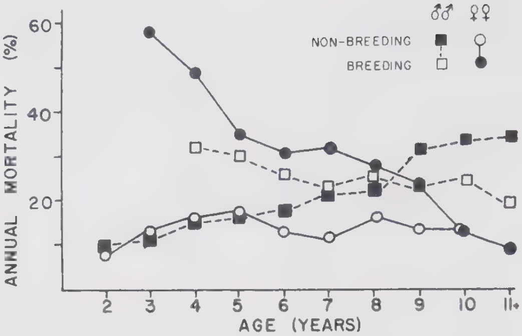

FIG. 4. Annual mortality of Adélies grouped by age, sex, and breeding status. The three-point moving averages are based on data in Table 9.

talities, three-point moving averages were calculated and are presented in Fig. 4. Mortality among breeding females declined from almost 75% in 3-yr-olds to 10% in those 11 yr and older (Table 9; $r = -.9653$, $P < .05$). Among nonbreeding females, mortality remained ≈12% ($r = .2538$, $P > .05$) throughout the age classes (female Adélies first breed at 3 yr; LeResche 1971). Mortality among breeding males also declined with age, from 36% in 4-yr-olds (the age of first breeding among male Adélies) to 18% in birds 11 yr and older ($r = -.8959$, $P < .05$), a change similar to that in females ($t = .050$, $P > .05$; test for homogeneity of regression, Steel and Torrie 1960:173). Among nonbreeding males, mortality increased from 7% in 2-yr-olds to 33% in birds 11 yr and older ($r = .8914$, $P < .05$).

Differences in annual mortality for birds of different age, sex, and breeding status relate to or affect the composition of Adélie populations in several ways. Among these, breeding status seems to be the most important controlling factor as the following analyses show, the data for which are presented in Table 9. The difference in annual survivorship between 1134 breeders (60.5%) and 697 nonbreeders (78.2%) regardless of sex, was highly significant (adjusted $\chi^2 = 37.8$, $P < .001$, df = 1). Age has a secondary effect on the mortality of breeders in that survival is very low in young breeders. Among 3- and 4-yr-old breeders ($n = 53$) annual survivorship was only 54.7% ($\sigma = 0.47$) compared to 72.5% ($\sigma = 0.02$) for breeders ($n = 1081$) 5–11+ yr of age (adjusted $\chi^2 = 8.79$, $P < .05$, df = 1). Age 5 yr was critical because there was no stiatistical difference when 3- to 5-yr-olds were compared with birds 6 yr of age and older. Mortality thus was high among breeders and especially high among the youngest two age classes. This is shown graphically in Fig.

TABLE 7. Partial horizontal life table for the Adélie Penguin. Data from Table 3 are averaged over both years of recovery.

Age (yr)	Number banded as chicks	Number recovered at age x	l_x
0	...	...	1.00
1	...	...	...
2	7 600	791	0.104
3	7 400	607	0.082
4	6 880	531	0.077
5	10 400	714	0.069
6	14 380	861	0.060
7	13 368	670	0.050
8	9 908	349	0.035
9	7 400	153	0.021
10	6 880	135	0.020
11	8 078	116	0.014
12	9 108	78	0.009
13	6 418	30	0.005
14	2 308	5	0.002

TABLE 8. Life table l_x values calculated by Ricklefs (1973) using Richdale's (1957) Yellow-eyed Penguin data, and corrected by the method of Payne (1977) for the fact that the population increased 230% during the study.

x (age in yr)	l_x*	“l_x”†
0	1.000	1.000
1	0.305	0.324
2	0.247	0.278
3	0.203	0.242
4	0.171	0.217
5	0.144	0.193
6	0.121	0.172
7	0.102	0.154
8	0.086	0.138
9	0.072	0.122
10	0.061	0.110
11	0.051	0.098
12	0.043	0.087
13	0.035	0.075
14	0.031	0.071
15	0.026	0.063
16	0.022	0.057

* l_x values from Ricklefs (1973: Table 4).
† “l_x” = $(l_x)(e^{rx})$, where $r = .059$.

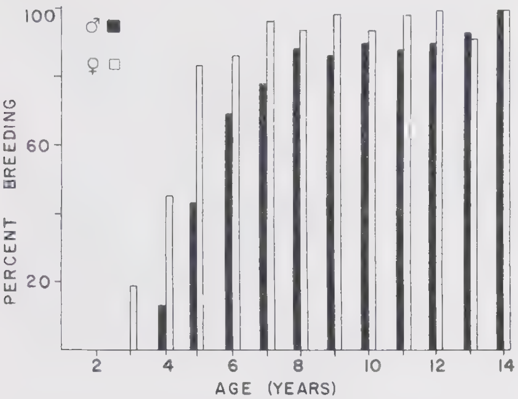

FIG. 5. The proportion of breeding individuals among male and female Adélies at each age.

4 where it also appears that for nonbreeders mortality increased only, if at all, among older individuals. A comparison of mortality between 10 yr and older nonbreeders (37.5%; $\sigma = 2.93$, $n = 8$) and younger nonbreeders (14.7%; $\sigma = 0.02$, $n = 633$) was not statistically significant (adjusted $\chi^2 = 1.63$), perhaps because the sample of older birds was not large enough.

The high mortality among breeders, especially young ones, the fact that females begin to breed earlier than males (average age of first reproduction for females, 4.70 ± 0.73, and for males, 6.80 ± 0.73; see DeMaster 1978), and the fact that a large proportion of older Adélie females (compared to males) breed (Fig. 5), led to higher mortality in females. This in turn led to a sex ratio that favored males more and more with greater age (Fig. 6) and accounted for the fact that the oldest Adélies were predominantly males. In fact, only 4 of 54 birds 10 yr or older were females (one 14-yr-old was a female). The sex ratio in Yellow-eyed Penguins changed in a similar but more gradual way ($t = 2.1392$, $P < .05$; test for homogeneity of regression, Steel and Torrie 1960:173); males predominated among the older birds but not to the same degree as in Adélie Penguins.

In light of these patterns, it is not surprising that the oldest Adélies shared the following characteristics: they tended to be males, they first bred at a late age, were nonbreeders during many of their years, and if they did attempt breeding were relatively unsuccessful (Ainley 1978; D. Ainley, R. LeResche, and W. Sladen, *personal observation*). Richdale (1957) did not provide information on whether a similar trend was true for *M antipodes*.

DISCUSSION

Annual survival among adult Adélies was much lower than in Yellow-eyed Penguins, particularly among younger birds. Part of the difference was due to the

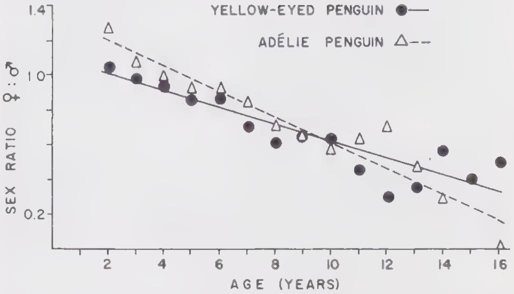

FIG. 6. The change in sex ratio with age within populations of Adélie and Yellow-eyed Penguins ($r = -.9532$ and $-.9056$, respectively).

Yellow-eyed Penguin population increase during Richdale's (1957) study whereas the Adélie Penguin population studied here was stable. The remainder of the difference was probably related in some way to the different lifestyles and environments of the two species. It may be that the harsher conditions during winter and the longer distances they traveled during both migration and feeding during the summer, led to a higher mortality among Adélies. The latter were also subject to a higher rate of predation (see below). The higher mortality among Adélie Penguins should have been compensated for by higher reproductive success. The data for comparison between the two species are not yet ready for analysis.

It appears that activities associated with reproduction are very costly for Adélie Penguins in terms of energy; in reproducing they increase their mortality substantially, especially the younger birds. Breeding in this species, as it must be in many other long-lived species, is an adjustment between not breeding at too young an age but breeding soon enough to insure reproduction. By breeding, a bird greatly increases the risks of an early death.

These compromises, as well as other factors, such as younger birds being less efficient at feeding (see Ainley and Schlatter 1972), must be related to the fact that Adélies do not become reproductively mature until at least 3 or 4 yr old (Ainley 1975). The majority, in fact, do not first breed until 4–6 yr and the proportion of birds breeding increases gradually with age, reaching 94% of birds 12 yr and older (Ainley 1978; Fig. 7). In contrast, the youngest Yellow-eyed Penguin breeders are 2 yr old and the proportion of adults breeding reaches its maximum as early as 4 yr. The proportion of breeders among birds at least 12 yr is significantly higher in Adélies (94%; $\sigma = 0.1$, $n = 92$) than in Yellow-eyed Penguins (81%; $\sigma = 0.1$, $n = 177$; $t = 3.365$, $P < .01$; test for percentages, Sokal and Rohlf 1969:608). The earlier age of youngest breeders and the much greater proportion of younger birds (3- to 5-yr-olds) breeding, indicates indirectly

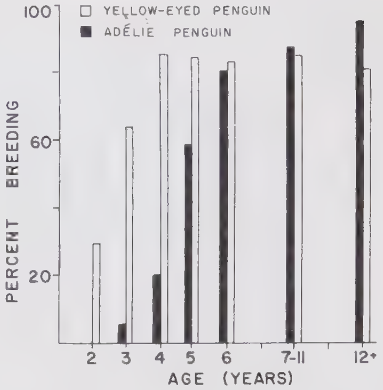

FIG. 7. The proportion of breeding individuals among Adélie and Yellow-eyed Penguins at each age. Some of the older age groups were combined to increase the samples. Data for Yellow-eyed Penguins are from Richdale (1949: Table 25).

that breeding at a young age is not as costly for Yellow-eyed Penguins. The Yellow-eyed Penguin sex ratio, which changes in a way similar to, but more gradual than that of Adélie Penguins, may suggest that mortality factors operate in the same way for the two species but at greater intensity for Adélies. This, plus the smaller proportion of birds 7 yr of age and older breeding in a given year, may account for the greater annual survival and longevity in Yellow-eyed Penguins.

Predation seems related closely to the high risk of breeding among Adélie Penguins. Predation by leopard seals (*Hydrurga leptonyx*) is well documented for Adélie Penguins (Penney and Lowry 1967, Müller-Schwarze and Müller-Schwarze 1975). These authors estimated that seals eat at least 1.4–5.0% of adults during the latter's breeding season each year. Based on a recent and more reliable but lower population estimate (Butler and Müller-Schwarze 1977), Adélie mortality due to predation within sight of the rookery is calculated at 2.3–7.3% of the adult population. Predation of Yellow-eyed Penguins by sea lions (*Neophoca hookeri*) also occurs (Spellerberg 1975, D. Ainley, *personal observation*) but has been reported very infrequently.

Leopard seals catch Adélies by waiting at the water's edge near the rookery. Several seals at Crozier are usually evenly spaced linearly along the beach. They also catch penguins in the ice pack during the summer but as far as we know this has been observed only once (D. Ainley, *personal observation*). Comparing the number of times breeding and nonbreeding Adélies must cross the line of leopard seals suggests one reason why breeding is so risky. To successfully rear young in an austral summer, breeders must pass through the seals an average of 47 times (data from Taylor 1962) but nonbreeders must pass through only four times (Ainley 1978). Since most of the trips occur in order to catch food for chicks, if the breeders lose their eggs or chicks early they are no longer "forced" to cope with the seals. Furthermore, nonbreeders (or unsuccessful breeders) are probably in better physical shape than breeders because during the few times that they leave the rookery, they are not pressured to feed and return quickly in order to relieve a mate or to tend chicks. If it is true that young breeders are less efficient at obtaining food, as suggested by Ainley and Schlatter (1972), then they may be less physically and energetically fit than older breeders. They may therefore fare even more poorly in coping with leopard seals. Because mortality is so high among the youngest Adélie breeders, 75% among 3-yr-olds and 40% among 4-yr-olds, one questions why Adélies risk breeding when so young, particularly at age 3 yr. The answer may be that birds breeding at 3 yr that survive tend to be highly productive breeders in subsequent years (D.

TABLE 9. Annual survivorship among Adélies of known age, sex, and breeding status.

	Breeders				Nonbreeders			
Age (yr)	Number ♂♂	Percent disappearing ±SD	Number ♀♀	Percent disappearing ±SD	Number ♂♂	Percent disappearing ±SD	Number ♀♀	Percent disappearing ±SD
2					112*	7 ± 2		
3			8	75 ± 15	78	13 ± 4	67	10 ± 4
4	11	36 ± 14	34	41 ± 8	79	14 ± 4	43	21 ± 6
5	113	27 ± 4	150	30 ± 4	117	17 ± 3	37	16 ± 6
6	152	27 ± 4	164	35 ± 4	62	18 ± 5	29	14 ± 6
7	145	25 ± 4	148	28 ± 4	32	19 ± 7	10	10 ± 9
8	38	18 ± 2	30	33 ± 9	8	25 ± 15	3	0 ± 0
9	22	32 ± 10	18	22 ± 10	7	0 ± 0	5	40 ± 22
10	28	21 ± 8	19	16 ± 8	3	67 ± 27	2	0 ± 0
11+	34	18 ± 7	20	10 ± 7	3	33 ± 27		
T	543		591		501		196	

* This number includes both males and females combined, as few were sexed.

Ainley, R. LeResche, and W. Sladen, *personal observation*). This then is the opposite extreme from those birds that by not breeding or by habitually breeding unsuccessfully reach a rather old age.

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Haematological characteristics of albacore, *Thunnus alalunga* (Bonnaterre), and skipjack, *Katsuwonus pelamis* (Linnaeus)

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Observations on haematological characteristics of albacore, *Thunnus alalunga*, and skipjack *Katsuwonus pelamis*, tunas, were made on blood samples collected from specimens immediately after they were caught and from an immobilized, restrained albacore sampled serially over a 24 h period. Results indicated eight types of blood cells in the peripheral circulation of both species. Lymphocytes were the most common leucocyte followed, in decreasing order, by neutrophils, eosinophils and monocytes in fish sampled immediately after being landed. Variations in differential and total white blood cell counts were observed in the immobilized, restrained albacore. High packed cell volumes and haemoglobin concentrations, typical for fast swimming fishes, were found in both species. Red blood cell counts were similar to those of other teleosts, and reticulocytes expressed as a percentage of mature erythrocytes were 6·1% and 5·2% for albacore and skipjack, respectively.

I. INTRODUCTION

Haemograms were made on blood samples from albacore, *Thunnus alalunga* (Bonnaterre), and skipjack, *Katsuwonus pelamis* (Linnaeus) tunas. Studies of erythrocytes included red cell counts, haemoglobins, packed cell volumes and reticulocyte counts. Leucocyte characterizations included white blood cell counts and differential cell counts. Cell measurements and morphological descriptions were also made.

There are only limited published reports regarding the blood characterizations of albacore and skipjack tunas. These reports deal primarily with haemoglobin values (Klawe, Barrett & Klawe, 1963; Barrett & Williams, 1965), packed cell volumes (Saito, 1954, 1959; Magnuson, 1969), and types and migration of haemoglobins (Sharp, 1969, 1973, 1975). Published information concerning leucocytes in tunas include a description of bluefin tuna, *Thunnus thynnus*, white cell morphology (Gutierrez, 1967) and cell count (Becker *et al.*, 1958), and tables containing differential counts for skipjack, little tuna, *Euthynnus alleterattus*, and yellowfin tuna, *Thunnus albacares* (Saunders, 1966; Saito, 1954). This paper will report haematological results observed as part of an investigation of albacore and skipjack tuna physiology and biochemistry.

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II. METHODS

Fish for blood sampling were caught by trolling or rod-and-reel during August 1977 and September 1978. Trolling was carried on at a speed of 5·5 knots and rod-and-reel fishing when the ship was stopped. Immediately upon a jig strike the ship was put out of gear and the fish reeled to it using a hydraulic gurdie. A dip net was used to bring on board fish caught using both fishing methods. The time required to land jig caught fish was usually about 1 min and to land rod-and-reel caught fish was 5–15 min.

Blood samples were collected by cardiac puncture with a 1 ml syringe using an 18 or 20 gauge needle immediately after the fish were brought on board. In some cases sea water was flushed over the gills of the fish during blood collection. Blood samples were also collected over a 24 h period from an albacore which was immobilized with Gallamine triethiodide (Flaxedil) to obtain information on haemogram profiles for use in studies to transport live albacore to holding facilities on shore. The fish was restrained and the gills were artificially irrigated with sea water beginning immediately after it was landed. A 0·4 ml dose of Flaxedil (20 mg per ml) was injected intravascularly promptly after the fish was brought on board and four additional 0·2 ml dosages were administered at various intervals during the sampling period. Blood samples were drawn through an indwelling catheter–stopcock system positioned in the upper, left subcutaneous vein. The initial blood sample was drawn approximately 13 min after the fish struck the lure. Subsequent sampling intervals and results are shown in Table III.

Blood samples from all fish were placed in pediatric EDTA tubes and mixed to prevent clot formation. In 1977 the analyses were performed aboard ship as soon as possible after collection, except reticulocyte and differential counts which were made on shore. In 1978 the samples were stored in EDTA tubes and held on ice for 9 to 18 h prior to being analyzed on shore.

In 1977 red cell counts were made according to the methods outlined by Hesser (1960) with fresh stains prepared daily. In 1978 a 1% Brilliant Cresyl Blue (BCB) solution diluted 1:1 with 0·85% saline was used instead of the solutions recommended by Hesser. Blood and diluent were mixed in red cell pipettes according to standard techniques. An improved Neubauer haemocytometer was used in making cell counts and the values were calculated using formulae given by Wintrobe (1974). White cell counts were made using methods outlined by Hesser (1960).

The cyanmethaemoglobin method was used to measure haemoglobins. Drabkins solution (Wintrobe, 1974) was prepared in 1977 and Becton-Dickinson haemoglobin unopettes were used in 1978. Standard curves were prepared from Hycel haemoglobin standard and percent transmittances of standards and samples were measured on a Coleman, Jr. or Beckman model DB spectrophotometer. Haemoglobin measurements were made on fresh albacore blood; however, haemoglobin measurements of skipjack blood were made on samples which had been frozen at −50° F for several weeks. Some precipitation occurred in the skipjack samples and they were centrifuged for 5 min at 5000 **g** to remove the precipitate prior to being read on the spectrophotometer. No precipitate was observed in the albacore blood-unopette solutions, which were colorimetrically stable over a 6 h period at ambient temperatures. Packed cell volume measurements were made in duplicate on blood samples collected in microhaematocrit tubes which were sealed with 'Critoseal' and centrifuged on a Clay Adams 'Autocrit' at 12 000 **g** for 5 min. Measurements were made on all cell types except reticulocytes, with an ocular micrometer. A minimum of 100 red cells and thrombocytes and 15 to 30 white cells were measured.

Differential blood counts were made on a minimum of two slides per fish sampled on the 1977 cruise. Blood smears were held for approximately 4 months prior to being stained and there was some loss of differential staining activity. The following steps described by Gallachio (1975) were used to enhance the staining quality of the smears. Smears were flooded with a 1% benzidine solution in absolute alcohol and allowed to react for 2 min. They were then lightly flooded with Superoxol (1 ml 30% H_2O_2 to 3 ml 70% ethanol), allowed to react for 2 min, flooded again with Superoxol, and allowed to react for another 2 min. The smears were then rinsed with tap water, air dried and stained with Wright's Giemsa (Harleco 'Diff-Quick'). Using this modification the cytoplasm of the red cells stained brown, providing a marked contrast between the brown cytoplasm of the nucleated red cells and the basophilic cytoplasm of the white cells and thrombocytes. A comparison of smears stained only with Wright's stain and those stained with the modified procedure showed that the modification did not interfere with the staining characteristics of the eosinophil granules or with the estimation of the age of red cells, as the younger red cells stained a lighter brown. One hundred white cells per slide were counted and classified. Thrombocyte counts were estimated by multiplying the mean thrombocyte count per field for 20 consecutive fields (1000 X) times 15 000. This method is currently used in human clinical laboratories as a means of cross-checking direct haemocytometer and automated thrombocyte counts. The number of reticulocytes per 1000 mature red cells was counted on smears from samples collected in 1977. The smears were made after allowing equal volumes of 1% BCB and blood to react for 10 min; reticulocyte identification was based on descriptions according to Dawson (1933). Photomicrographs were made of representative cell types using a tungsten light source without filters and Kodak Ektachrome EH 135-36 film at a magnification of 1000 X.

III. RESULTS AND DISCUSSION

CELLULAR OBSERVATIONS

The literature dealing with fish haematology is often confusing because of the lack of uniformity in morphological criteria and terminology applied to blood cell identification. This contributed to difficulties encountered in this study, especially in the identification of white cells. Ellis (1977) discusses these problems in detail.

Eight types of blood cells were recognized in albacore and skipjack tunas: reticulocytes, mature erythrocytes, thrombocytes, neutrophils, lymphocytes, monocytes, eosinophils and an eosinophil-like cell. Information on mean size and distinguishing features of the blood cells are summarized in Table I. The morphology of the skipjack cells was nearly the same as for albacore except: (1) the red cells were smaller, $8{\cdot}0 \times 6{\cdot}4\ \mu m$; and (2) the lymphocytes and thrombocytes were larger, $6{\cdot}3 \times 5{\cdot}5$ and $6{\cdot}7 \times 4{\cdot}0\ \mu m$, respectively. The morphology of the albacore and skipjack blood cells closely resembled those of bluefin tuna as described by Gutierrez (1967).

Leucocytes

The lymphocytes in albacore and skipjack were similar in appearance to those reported in other teleosts, although a range of sizes was observed rather than 'small' and 'large' as has been reported for some other species (Saunders, 1966; Gutierrez, 1967; Ellis, 1977). Monocytes were present in low numbers in both albacore and skipjack. They were the largest cell in the peripheral circulation of both species and typically contained one or more vacuoles in the cytoplasm. A variety of nuclear configurations have been reported for neutrophils from teleosts (Saunders, 1966; Conroy, 1972; Ellis, 1977). The most prevalent form observed in our studies was an eccentric, monolobed nucleus; however, occasionally a bilobed nucleus was noted. The cytoplasm had a 'ground-glass' appearance, created by the presence of many fine, faintly grey-pink granules. Basophils were not observed in either albacore or skipjack, which is in agreement with earlier observations on skipjack (Saito, 1954; Saunders, 1966), little tuna (Saunders, 1966), and yellowfin tuna (Saito, 1954). This observation also agrees with Becker *et al.* (1958) who did not observe basophils in bluefin; however, it does not agree with Gutierrez (1967), who reported basophils to be the smallest and most scarce

TABLE I. Size range and distinguishing features of the blood cells of the albacore tuna

Cell type	Number of cells measured	Nucleus	Cytoplasm and cell outline	Mean size of cells (μm)
Reticulocytes	—	Oval; slightly larger and more rounded than in mature red cells; chromatin less pyknotic than in mature red cells; basophilic	Circular; more polychromatophilic than mature red cells; in benzidene-treated smears, cytoplasm much lighter brown than in mature red cells	—
Erythrocytes	100	Elliptical; basophilic, chromatin pyknotic	Elliptical; polychromatophilic with varying degrees of polychromasia; in benzidene-treated smears cytoplasm brown; inclusion bodies present in most cells tending to form ring around nucleus	9·0 × 6·6
Thrombocytes	100	Elliptical; homogeneous; basophilic; takes up major portion of cell; occasionally slightly indented	Spindle-shaped; cytoplasm appears as a blue-grey, thin rim; punctate, clear areas sometimes observed in cytoplasm at top of nucleus or bilaterally next to nucleus in centre of cell	4·7 × 3·0
Neutrophils	20	Irregularly elliptical, eccentric; appears red-purple; chromatin lattice-like appearance and slightly clumped	Irregularly elliptical; appears blue-grey; cytoplasm occasionally contained fine, sand-like particles imparting a ground glass appearance	8·6 × 7·9
Lymphocytes	30	Irregularly elliptical; homogeneous; appears red-purple; takes up major portion of cell	Irregularly elliptical; cytoplasm in narrow rim around cell; strongly basophilic; occasional azurophilic granules observed	5·7 × 5·2
Eosinophils	20	Oval; eccentric; chromatin slightly clumped and appears red-purple	Oval to elliptical; cytoplasm filled with discrete, rod-shaped eosinophilic granules	8·9 × 5·0
Eosinophil-like	10	Oval; eccentric; homogeneous; basophilic	Oval to elliptical; cytoplasm faintly eosinophilic, but no discrete granules apparent	6·6 × 5·0
Monocytes	15	Oval; eccentric, chromatin clumped and appears red-purple	Oval; appears grey-blue; rough and bumpy in appearance, frequently containing one or more vacuoles	10·5 × 9·5

of the granulocytes present in bluefin tuna. It is possible that basophils could be present in low numbers in the peripheral circulation of albacore and skipjack, yet not be in the smears which we examined. Eosinophils were present in both the skipjack and albacore and their occurrence has been reported in many other fishes (McKnight, 1966; Saunders, 1966; Gutierrez, 1967; Ellis, 1977, and others). Saunders mentions the presence of 'large' and 'small' eosinophils in the skipjack, but did not give comparative sizes; this phenomenon was not observed in our study.

A cell similar in appearance to, but smaller than, the eosinophil was observed in low numbers in both species. The nucleus was eccentric, homogeneous and basophilic. The cytoplasm appeared eosinophilic, but lacked the granules which typify the eosinophil. The eosinophil-like cell observed in this study somewhat resembled a cell first characterized by Downey (1909) from the kidney tissue of paddle fish (*Polydon spathula*) and later described by Saunders (1966). However, until further studies are performed, its exact classification remains unknown.

Thrombocytes

The thrombocytes of both the albacore and skipjack were typically elliptical cells with thin rims of pale blue cytoplasm, with those of the albacore being smaller and more rounded than those of the skipjack. The cytoplasm occasionally contained vacuoles or peri-nuclear clear areas similar to those reported for bluefin tuna by Gutierrez (1967). Ellis (1977) cites several authors who have reported four thrombocyte maturation stages present in the peripheral circulation of different fish species. This was not observed in this study, although several basophilic 'lone nuclei' forms were noted, which appeared more like erythrocytic precursors (Catton, 1951) than like immature thrombocytes. Thrombocytes were more abundant in albacore than skipjack, averaging 44 380 mm^{-3} and 28 880 mm^{-3}, respectively (Table II).

Erythrocytes

The red cells of the albacore and skipjack were elliptical, elongated and nucleated with perinuclear granules. The granules are believed to be of cytoplasmic origin and associated with the formation of haemoglobin (Dawson, 1933). The reticulocytes, when observed with a supra–vital stain and in contradistinction to the mammalian non–nucleated immature red cells, were more rounded than the mature cells. The reticulum formed a loose, disconnected mesh around the nucleus when observed in supra–vital stained smears. The cytoplasm appeared more polychromatophilic in the reticulocyte than in the mature erythrocyte when observed in Wright's stained smears.

WHITE CELL COUNTS

Direct counts of total white blood cells were attempted, but the results are considered questionable due to cellular clumping, stain precipitation and variable staining. The limited data we collected suggest that total white cell counts were relatively low in both species, ranging from approximately 2000 to 10 000 mm^{-3}. A decreasing trend in the total white cell count was noted over the approximately 24 h period that the immobilized, restrained albacore was sampled (Table III).

TABLE II. Summary of erythrocytic data for albacore and skipjack tunas

	Albacore								Skipjack			
	Group I (1977)				Group II (1978)							
	Sample size	Range	Mean	Std.	Sample size	Range	Mean	Std.	Sample size	Range	Mean	Std.
Length (cm)	17	55–77†	66	7·4	16	80–90*	87	—	15	52–57	55	2·2
Weight (kg)	17	3·3–8·2	5·7	1·8	16	10·1–14·2*	12·9	—	15	2·5–4·5	3·5	0·52
Packed cell volume (%)	23	42–57	49·8	4·48	29	53–63	58·2	2·99	15	42–66	59·3	5·98
Haemoglobin (g/dl)	16	11·0–17·8	15·0	1·50	29	15·0–17·8	16·3	0·63	6	15·8–22·3	18·0	2·38
Mature erythrocytes ($\times 10^6$ mm^{-3})	17	2·65–4·36	3·17	0·48	15	2·31–2·95	2·60	0·22	15	2·5–4·8	4·14	0·64
Reticulocytes (%)†	14	3·33–9·03	6·10	1·62		(no observations)			9	2·39–9·97	5·20	2·38
Thrombocytes ($\times 10^4$ mm^{-3})	5	33–69	44·38	16·29		(no observations)			5	22–26·5	28·88	3·58

*Estimated; †Expressed as percentage of mature erythrocytes.

TABLE III. Summary of haematological data for an immobilized, restrained albacore sampled over approximately 24 h period

Time	Sampling interval	Packed cell volume (%)	Haemoglobin (g/dl)	Red blood cells (× 10^6 mm^{-3})	White blood cells (× 10^3 mm^{-3})	Neutrophils	Differentials (%)		Eosinophils
							Lymphocytes	Monocytes	
07.54	0*	55·5	17·8	3·47	7·8	10	71	5	14
08.44	50″	52·5	16·9	3·90	10·6	4	88	2	6
09.45	1′51″	50·5	16·2	3·66	8·8	8	84		8
10.39	2′45″	51·5	15·3	3·87	7·2	12	72		16
11.49	3′55″	50·0	19·4	3·63	5·4	14	68		18
13.21	5′21″	49·5	17·7	3·82	6·0	4	60	4	32
14.34	6′40″	47·5	16·5	3·45	5·1	8	62		30
17.34	9′40″	46·0	13·3	3·37	4·0	16	68		16
20.35	12′31″	41·0	14·9	3·10	4·4	4	76		20
05.55	22′01″	59·0	19·5	4·25	2·7	24	50		26
07.05	23′11″	58·5	20·2	3·96	2·0	6	74	4	16

*Initial sample taken approximately 13 minutes after fish struck lure, fish caught on rod and reel and landed in approximately one minute.

TABLE IV. Differential counts for albacore and skipjack sampled in 1977

Cell type	Albacore		Skipjack	
	Mean*	Range	Mean*	Range
Neutrophils	24	0–80	33	10–98
Lymphocytes	51	0–92	46	2–92
Eosinophils	13	0–28	11	0–24
Eosinophil-like	6	0–12	4	0–10
Monocytes	6	0–20	6	0–12

*Mean values weighted so sum equals 100.

DIFFERENTIAL BLOOD CELL COUNTS

In albacore and skipjack sampled immediately after being brought on board, lymphocytes were the most common leucocyte in the peripheral circulation, followed in decreasing order by neutrophils, eosinophils and monocytes (Table IV). In the albacore sampled over time, lymphocytes were also the most prevalent white cell in the peripheral circulation; however, eosinophils were more abundant than neutrophils and tended to increase with time, while the total white cell count appeared to decrease (Table III).

A selected review of recent literature reveals that some authors include thrombocytes in differential white cell counts (Boyar, 1962; Saunders, 1966; Gardner & Yevich, 1969; Sherbourne, 1973; McCarthy, Stevenson & Roberts, 1973, 1975) while others do not (Becker *et al.*, 1958; Watson *et al.*, 1963; Colgrove, 1966; Pitombeira & Martins, 1970; Blaxhall, 1972; Conroy, 1972). We have followed the convention used in mammalian studies and did not include thrombocytes in the differential white cell counts. While a direct comparison with published differential counts is difficult, our differential counts are generally consistent with those reported in the literature. The high lymphocyte counts we found in albacore and skipjack agree with results reported for bluefin tuna (Becker *et al.*, 1958), little tuna (Saunders, 1966), mackerel (Becker *et al.*, 1958; Pitombeira & Martins, 1970) and other teleosts (Watson *et al.*, 1963; Mulcahy, 1970; McCarthy *et al.*, 1973, 1975, and others). The increase in circulating eosinophils observed over time in the restrained, immobilized albacore is similar to findings made by Gardner & Yevich (1969) who noted increases in eosinophil levels over time in *Fundulus heteroclitus,* which the authors judged were stressed because the fish were held in small aquaria. They also found that specimens held in large aquaria showed little change in the eosinophil level over time.

ERYTHROCYTIC CHARACTERISTICS

A summary of erythrocytic data observed for albacore and skipjack tunas sampled immediately after being brought on deck is presented in Tables II and V, and for the immobilized albacore sampled serially over approximately 24 h in Table III. The erythrocytic results found in this study are in agreement with published data for tunas, which have been summarized in Table V.

Red blood cell counts

We found mean red blood cell counts of $3{\cdot}17 \times 10^6\ \text{mm}^{-3}$ (1977) and $2{\cdot}60 \times 10^6\ \text{mm}^{-3}$ (1978) for albacore and $4{\cdot}14 \times 10^6\ \text{mm}^{-3}$ for skipjack (Table II). The red cell counts of the immobilized albacore sampled serially over approximately 24 h ranged from $3{\cdot}10 \times 10^6\ \text{mm}^{-3}$ to $4{\cdot}25 \times 10^6\ \text{mm}^{-3}$ (Table III). These values are similar to those reported in the literature for tunas (see Table V).

The difference in mean red cell counts for albacore observed in 1977 and 1978 is statistically significant ($P = 0{\cdot}005$). This difference could be related to numerous contributory factors. For example, based on albacore tagging data and fishery data collected during the two years, it appears that the fish sampled in 1978 had immigrated into the area of capture and remained there several weeks longer before capture than had the fish sampled in 1977. There may, therefore, have been differences in migratory status, diet, and nutritional status in the fish sampled in the two years. Also, the fish sampled in 1978 were about twice the mean size of the fish sampled in 1977 (Table II). The effect of size, if any, on albacore red cell counts is not known. Gutierrez (1967, 1970) reported results for bluefin tuna that suggest a relationship between spawning and red cell count. He observed lower red cell counts in pre-spawning individuals than in post-spawning individuals.

Reticulocytes

The mean number of reticulocytes in the peripheral circulation, expressed as a percentage of the mature erythrocytes, was 6·1% in albacore and 5·2% in skipjack. We found no published data on reticulocyte counts for tunas and only a few reports for other teleosts. Dawson (1933) reported the proportion of circulating immature erythrocytes in what he termed 'active' fishes, which included the Atlantic mackerel, *Scomber scombrus*, as approximately 20%, in less 'active' fishes as 3–6%, and in relatively sluggish fishes as few or rare. Dawson's study was conducted on fishes held in aquaria and he notes that in general the group of fish he included as 'active' are characterized by their inability to survive for any extended period in restricted quarters, and that the sensitivity to confinement could be a factor in his results. Catton (1951) reported that reticulocytes formed 1–2% of the erythrocyte population in three freshwater and two marine species of fishes. Watson *et al.* (1963) noted that immature erythrocytes are frequently encountered in the blood of healthy goldfish, *Carassius auratus*, and do not indicate a blood dysfunction.

Haemoglobin values

We found mean haemoglobin values of 15·0 g/dl (1977) and 16·3 g/dl (1978) for albacore and 18·0 g/dl for skipjack (Table II). These values are comparable with those observed in tunas by other investigators (Table V). Haemoglobin values for the immobilized albacore ranged from 13·3 g/dl to 20·2 g/dl with minimum values occurring at the same sampling times, 9·40 hours and 12·31 hours, as the minima in red blood cell counts (Table III).

Packed cell volume

Mean packed cell volume values (PCV) for albacore were 49·8% (1977) and

TABLE V. Summary of published red blood cell counts, haemoglobin concentrations and packed cell volumes observed in tunas and mackerels

Species		Red blood count (× 10⁶)			Haemoglobin (g/dl)			Packed cell volume (%)		
Scientific name	Common name	Number	Mean	Range	Number	Mean	Range	Number	Mean	Range
Thunnus alalunga	Albacore									
Present study		17	3·17	2·65–4·36	16	15·0	11·0–17·8	23	49·8	42–57
		15	2·60	2·31–2·95	29	16·30	15·0–17·8	29	58·4	53–63
Barrett and Williams (1965)					11	17·97	15·3–19·3			
Thunnus thynnus	Bluefin tuna									
Gutierrez (1970)		10	2·85	2·1–4·1	10	17·3	15·2–20·5	10	52·8	50–57
		10	2·35	1·9–3·4	10	16·2	14·8–19·2	10	51·1	43–56
Gutierrez (1967)		12	2·15	1·8–2·4	12	15·4	15·0–16·0	12	52·4	50–55
		10	1·95	1·8–2·04	10	14·9	14·5–15·3	10	51·0	46–58
Barrett and Williams (1965)					10	19·8	18·7–21·0			
Becker et al. (1958)		—	2·3	—				—	41·0	—
Thunnus albacares	Yellowfin tuna									
Barrett and Williams (1965)					8	16·8	15·3–19·3			
Klawe et al. (1963)					11	—	15·8–18·9			
Barrett and Conner (1962)					22	14·3	11·5–16·5			
Saito (1959)		18	3·87	—	18	14·4	—	18	51·5	—
Saito (1954)		—	3·64	—	—	14·9	—	—	50·1	—
Thunnus obesus	Bigeye tuna									
Barrett and Williams (1965)					25	15·6	10·3–20·8			
Katsuwonus pelamis	Skipjack tuna									
Present study		15	4·14	2·5–4·8	6	18·0	15·8–22·3	15	59·3	42–66
Magnuson (1969)					21	16·1	—	21	56·2	—
Klawe et al. (1963)					9	—	14·1–20·7			
Barrett and Conner (1962)					21	16·7	15·0–18·5			
Saito (1959)		24	3·92	—	24	14·1	—	24	53·3	—
Saito (1954)		—	3.396	—	—	14·4	—	—	48·3	—

Euthynnus lineatus	Black skipjack									
Klawe et al. (1963)					5	—	16·9–19·9			
Sarda chiliensis	Pacific bonito									
Barrett and Williams (1965)					9	12·9	11·2–15·3			
Klawe et al. (1963)					14	—	8·3–14·8			
Auxis rochei	Frigate mackerel									
Barrett and Williams (1965)					10	19·2	16·5–22·8			
Klawe et al. (1963)					6	—	17·8–21·2			
Scomber scombrus	Atlantic mackerel									
Larsen et al. (1976)					3	12·7	—	3	52·5	—
Scomber japonicus	Pacific mackerel									
Klawe et al. (1963)					10	—	8·0–14·8			
Scomber australasicus	Spotted chub mackerel									
Saito (1959)		27	3·80	—	27	13·8	—	27	50·6	—
Saito (1954)		—	3·51	—	—	13·9	—	—	47	—
Scomberomorus maculatus	Spanish mackerel									
Pitombeira and Martins (1970)		100	3·48	1·5–5·43	100	11·1	6·4–15·0	100	47	34–61
Engel and Davis (1965)		58	4·54	3·15–6·13	58	10·4	7·6–12·2	58	38·8	26·5–48·0
Becker et al. (1958)		—	3·2	—				—	38	—
Scomberomorus regalis	Cero									
Swarts (1969)					1	12	—	1	44	—
Scomberomorus cavalla	King mackerel									
Engel and Davis (1965)		6	3·54	2·66–4·59	6	9·3	7·3–10·3	6	36·3	32–43

58·2% (1978) and for skipjack was 59·3% (Table II). These values are similar to those reported in the literature for tunas (Table V). The PCV values for the immobilized albacore showed a gradual decrease from an initial value of 55·5% to a minimum of 41·0% at the 12·31 hours sampling time. The final two packed cell volumes sampled at 22·01 hours and 23·11 hours, were elevated to 59·0% and 58·5%, respectively (Table III).

Little is known about the ranges and variation of 'normal' haematologic values for the tunas. The results presented in this manuscript are intended to assist research workers in establishing ranges of normal haematologic values for albacore and skipjack tunas. This information is necessary before haematological data can be used to accurately assess physiological status in tunas. Many factors may contribute to variations in haematological parameters of fishes and must be evaluated for the tunas. These factors may be grouped into categories including: (1) those which can cause individual haematological differences *in vivo* in tunas, e.g. age, sex, migration, season, environmental conditions, etc.; (2) those which are due to stress resulting from capture, handling and sampling procedures; and (3) those due to the inaccuracy of analytical methods, identifications, etc.

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ALVARIÑO: DISTRIBUTION OF ZOOPLANKTON PREDATORS AND ANCHOVY LARVAE
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THE RELATION BETWEEN THE DISTRIBUTION OF ZOOPLANKTON PREDATORS AND ANCHOVY LARVAE

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ABSTRACT

Monthly CalCOFI cruises of 1954, 1956, and 1958 were analyzed for abundance of populations of species of Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. Data were also noted on other abundant zooplankters in the samples (copepods, euphausiids, decapod larvae, pteropods, heteropods, polychætes, salps, doliolids, and pyrosomes). Information was grouped into three categories of abundance of anchovy larvae per standard haul (more than 241 anchovy larvae, from 1 to 240, and absence of larvae). In general, concentration of predators was inversely related to aggregations of anchovy larvae. Absence of anchovy larvae coincided with prochordates, decapod larvae, pteropods, heteropods, and polychætes, and abundance of anchovy larvae concurred with abundance of copepods and/or euphausiids. This habitat can be designated "anchovy water."

Gut content analysis indicated that predatory pressure on fish larvae was weaker when there was abundance of other food animals, e.g. copepods and euphausiids in the waters, as shown by the plankton collections.

RESUMEN

Las poblaciones de especies de Quetognatos, Sifonóforos, Condróforos, Medusas y Ctenóforos han sido analizadas en las colecciones de plancton obtenidas durante los cruceros mensuales de CalCOFI en 1954, 1956 y 1958. Conjuntamente se anotaron datos sobre la abundancia de otros zooplanctones presentes en esas muestras de plancton (Copépodos, Eufáusidos, larvas de Decápodos, Pterópodos, Heterópodos, Poliquetos, Salpas, Doliolos y Pirosomas). La información obtenida sobre la abundancia de las especies correspondientes, se ha agrupado en tres categorías, en relación con la cantidad de larvas de anchoa en cada arrastre (más de 241 larvas, desde 1 hasta 240, y ausencia de larvas). En general, la concentración de depredadores y larvas de anchoa aparecía en relación inversa. Se observó con frecuencia, que en las zonas de surgencia no aparecían larvas de anchoa. La ausencia de larvas de anchoa coincidía con la presencia de Procordados, larvas de Decápodos, Pterópodos, Heterópodos, y Poliquetos, y la abundancia de larvas de anchoa concurría con gran cantidad de Copépodos y Eufáusidos. Este hábitat podría denominarse "agua de anchoa."

Los análisis del contenido estomacal de los depredadores y las correspondientes muestras de plancton han demostrado que cuando abundaban en el plancton copépodos y eufáusidos, los depredadores ingerían menos larvas de peces.

INTRODUCTION

Mortality of pelagic marine fish larvae can result from a variety of causes, both biotic and abiotic. Among the more important biotic causes are starvation, predation, parasites, and disease; among the abiotic causes are storms, currents, ultraviolet radiation, temperature, salinity, oxygen, and pollution. It was the consensus of participants in a Colloquium on Larval Fish Mortality Studies, held in La Jolla during January of 1975, "that the major causes of larval mortality are starvation and predation, and that these may interact" (Hunter 1976). It was noted in the report that most research emphasis had been placed on starvation and relatively little work existed on predation. Observations on predation of invertebrate plankton organisms on fish larvae appear in Lebour (1922, 1923, 1925), Bigelow (1926), Fraser (1969), Dekhnik et al. (1970), and others, as discussed in Alvariño (1976, 1977).

Several recent laboratory studies have dealt with invertebrate predation on newly hatched larvae of the northern anchovy: copepods as predators (Lillelund and Lasker 1971) or the euphausiid *Euphausia pacifica* in Theilacker and Lasker (1974). These predators are most effective on the relatively passive yolk-sac larvae of the anchovy and less so on actively swimming larger anchovy larvae. The principal planktonic predators on large anchovy appear to be Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. Predation by these zooplankters has been observed frequently by planktologists, who find fish larvae in various stages of digestion inside the guts of these predators. Despite such observations, no one has attempted a thorough analysis of such predation on fish larvae.

It is the purpose of this contribution to study the relation between occurrence and abundance of anchovy larvae (*Engraulis mordax*) to the other elements in the plankton, with emphasis on potential predators, and also to characterize the assemblages of plankters in relation to anchovy larva abundance. The monthly CalCOFI collections made off California and Baja California in 1954, 1956, and 1958 were selected for this study. These three

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years were respectively, slightly colder, colder, and warmer than the long-term average for the California Current region. One reason for reanalyzing field collections of plankton rather than doing experimental studies in the laboratory on Chætognatha, Siphonophoræ, Chondrophopæ, Medusæ, and Ctenophora as predators is that these organisms are difficult subjects for experiments. They lack the capacity for food reserve storage, for example, hence must feed continuously to avoid starvation. The reason for limiting the study to anchovy larvae while ignoring occurrence and abundance of anchovy eggs is that the eggs are less exposed to predation by these predators, which respond primarily to movement.

METHODS

The plankton collections analyzed were from the monthly cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for 1954, 1956, and 1958. The area covered was the California Current region off California and Baja California, with usual coverage between San Francisco, off central California, to Cape San Lazaro, off southern Baja California (CalCOFI lines 60 to 137). The plankton was collected with a bridled net, 1 m in diameter at the mouth, about 5 m in length, constructed of heavy-duty bolting grit gauze of 50xxx mesh. The nets were equipped with flow meters to measure the volume of water strained during each tow. The hauls were made obliquely from about 140 m to the surface, depth of water permitting.

The total plankton sample was analyzed for the five groups of predators: Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. It should be pointed out that Ctenophora are often destroyed by preservation, hence the numbers recorded are underestimates of their true abundance in the collections. In all five groups, specimens present in each sample were identifed to species and counted by species. Only occasionally, when a species occurred in large numbers, were counts made on an aliquot of the total sample. Numbers of each species were standardized to the number in 1,000 m^3 of water strained. In addition, the size of each specimen in mm was recorded, together with stage of sexual maturity and/or stage of life cycle. Also, the number of specimens with food in the stomachs was noted, and partially digested organisms were identified. It is supposed that many of these predators fill their guts while in the plankton net, hence presumed newly ingested organisms were not considered. Table 5, which is not included in this report, but is available from the author upon request, detailed the assemblages of plankton at selected locations in the anchovy larvae realm, with absence of anchovy and highest concentration of anchovy larvae, for the monthly cruises of 1954, 1956, 1958. Also in this Table appear for each selected station the abundance of each of the species of Chætognatha, Siphonophoræ, Medusæ, Ctenophora; the presence of copopods, euphausiids, pteropods, heteropods, decapoda larvae, polychætes, tunicates; and information on the volume of water strained per haul.

During the analysis of the collections of the three years, it was observed that approximately 36% of the chætognaths had food in their stomachs, and all specimens of the two largest species, *Sagitta hexaptera* and *S. scrippsae*, contained food in many collections. Some chætognath stomachs contained prey not present in the corresponding plankton samples.

Data also were taken on the relative abundance of the various constituent groups in each sample. The groups included, in addition to the five groups of predators discussed above, were copepods, euphausiids, decapod larvae, pteropods, heteropods, polychætes, salps, doliolids, and pyrosomes. The determinations were based on dominance of a group or groups in the collections analyzed.

Although initially it was proposed to analyze all samples taken during the three years, 1954, 1956, and 1968, this soon proved to be too large a task. Instead, emphasis was placed on the areas that contained anchovy larvae in some abundance, in order to determine areal and temporal coverages that would bear most directly on the problem of predator-anchovy interactions. The collections used in the following analyses were 849 for 1954, 316 for 1956, and 899 for 1958.

Anchovy abundance was divided into three categories on the basis of abundance in the tows: high, low, and zero. The standard haul values of anchovy larvae in the high category corresponded to 241 larvae or more per haul. The standard haul value is the estimated number of anchovy larvae under 10 m^2 of sea surface. The count of low abundance included all positive hauls with counts lower than 241 larvae per standard haul. Inasmuch as the average CalCOFI haul sampled to about 140 m depth, the actual volume of water involved under 10 m^2 of sea surface is approximately 1,400 m^3. Although the number of anchovy larvae is not ordinarily expressed as the number in 1,000 m^3 water strained, the unit of volume used for zooplankters would be about 10/14 that of anchovy larvae on the average, or approximately 172 larvae or more for the high category of anchovy larvae abundance.

KINDS AND ABUNDANCE OF PREDATORY SPECIES IN THE FIVE CATEGORIES BEING STUDIED

A list of the species encountered by category, number of individuals taken and number of positive hauls (occurrences) of each species by year, and information on size and depth distribution of each species is contained in Table 1. The information included in this table, such as the kinds and abundance of the species of chætognaths,

TABLE 1

Abundance of Predatory Species (Frequency, In Parentheses) with Information on Size and Depth Distribution[1]

	Total number (and frequency)			~Maximum size			
Species	1954 (849 hauls)	1956 (316 hauls)	1958 (899 hauls)	(mm)	Nect.	cm complete animal	Depth distribution
Eukrohnia bathypelagic, Alvariño 1962		34(1)		23			Upper 100 m during upwelling
E. hamata (Möbius) 1875		43(1)		43			Upper 100m during upwelling
Krohnitta pacifica (Aida) 1897	464(20)		943(40)	8			Upper 100 m
K. subtilis (Grassi) 1881	5402(144)	2186(29)	5735(242)	16			Upper 100 m to surface
Pterosagitta draco (Krohn) 1895	5189(175)	1761(43)	13531(350)	10			Upper 100 m to surface
Sagitta bedoti Beraneck 1895	528(5)		2797(12)	15			Upper 100 m to surface
S. bierii Alvariño 1961	785319(712)	235853(210)	481090(700)	17			Upper 100 m to surface
S. bipunctata Quoy and Gaimard 1827	10870(244)	2969(43)	32665(384)	18.5			Upper 100 m to surface
S. decipiens Fowler 1905	3446(12)	3184(35)	1744(46)	16			Upper 100 m during upwelling
S. enflata Grassi 1881	366890(511)	43618(135)	831089(794)	25-30			Upper 100 m to surface
S. euneritica Alvariño 1961	2052102(616)	592934(284)	983727(485)	15.5			Upper 100 m to surface
S. hexaptera d'Orbigny 1834	10941(422)	2599(157)	14009(477)	40-60			Upper 100 m to surface
S. maxima (Conant) 1896		184(12)		>90			Upper 100 m during upwelling
S. minima Grassi 1881	250862(625)	44374(217)	300710(662)	10			Upper 100 m to surface
S. neglecta Aida 1897	606(12)		466(13)	8			Upper 100m to surface
S. pacifica Tokioka 1940	8664(84)	3137(26)	25187(256)	14			Upper 100 m to surface
S. pseudoserratodentata Tokioka 1936	40940(248)	6301(36)	92194(420)	10			Upper 100 m to surface
S. pulchra Doncaster 1903			23(1)	24			Upper 100 m to surface
S. regularis Aida 1897	1996(22)		5065(54)	6			Upper 100 m to surface
S. robusta Doncaster 1903	179(6)		1539(24)	12			Upper 100 m to surface
S. scrippsae Alvariño 1962	52289(443)	13903(169)	11192(169)	60			Upper 100 m to surface
S. zetesios Fowler 1905		24(1)		43			Upper 100 m during upwelling
Agalma okeni Eschscholtz 1825	25(5)	37(13)	58(18)		20	>100	Surface and depth
Nanomia cara Agassiz 1865		5(1)			>51	>100	Surface and depth
Stephanomia bijuga (Delle Chiaje) 1841	552(59)	1157(101)	210(43)		15	>100	Surface and depth
Bargmannia elongata Totton 1954		82(5)	11(1)		30	>100	Surface and depth
Physophora hydrostatica Forskal 1775		56(15)	19(6)		8	12	Surface and depth
Erenna richardi Bedot 1904			3(1)		40	>100	Surface and depth
Epibula ritteriana Haeckel 1888	15(2)	3(1)				6	Surface
Rosacea cymbiformis 1841 Chiaje	6(2)	11(2)	3(1)		350	many	Surface and depth
R. plicata Quoy and Gaimard 1827	6(2)	12(2)			200	many	Surface and depth
Nectodroma dubia Quoy and Gaimard 1834	3(1)	88(4)	6(2)		85	many	Upper 100 m
N. reticulata Bigelow 1911		2(1)			55	many	Upper 100 m
Nectopyramis thetis Bigelow 1911			3(1)		40	many	Upper 100 m and depth
Lilyopsis rosea Chun			6(2)		120	many	Upper 100 m and depth
Amphicaryon acaule Chun 1888	6(2)	9(2)			>15	many	Upper 100 m and depth
A. ernesti Totton 1954	18(4)	9(1)	6(1)		>15	many	Upper 100 m and depth
Hippopodius hippopus Forskal 1776	3(1)	20(6)	18(6)		19	many	Surface and depth
Vogtia kuruae Alvariño 1967		3(1)			20	many	Surface and depth
V. spinosa Kefferstein and Ehlers 1861		40(2)			20	many	Surface and depth
Chelophyes appendiculata Eschscholtz 1829	15819(145)	7079(160)	14628(154)		10	2	Upper 100 m to surface
C. contorta (Lens and Riemsdijk) 1908	83(3)	7(1)	2622(20)		7	14	Upper 100 m to surface
Dimophyes arctica Chun 1897		23(2)			13		Upper 100 m to surface
Diphyes bojani (Eschscholtz) 1829		12(3)	562(150		15	3	Upper 100 m to surface
D. dispar Chamisso and Eysenhardt 1821	19802(89)	614(9)	150(6)		20	4	Upper 100 m to surface
Diphyopsis mitra Huxley 1859	79(3)	105(5)	2243(22)		10	2	Upper 100 m to surface
Muggiaea atlantica Cunningham 1892	25117(123)	29565(165)	11495(95)		7		Surface
Eudoxia macra Totton 1954	916(8)	366(12)	808(12)		4		Surface
Eudoxoides spiralis Bigelow 1911	1008(15)	617(12)	16690(64)		7		Upper 100 m to surface
Sphaeronectes sp.	29(2)	135(6)	155(8)		8		Upper 100 m to surface
Lensia campanella Moser 1925			279(4)		6	1	Upper 100 m to surface
L. challengeri Totton 1954	14366(69)	17862(99)	7236(77)		9	1.7	Upper 100 m to surface
L. conoidea Kefferstein and Ehlers 1861	53(3)	695(30)	267(12)		20	4	Upper 100 m and depth
L. grimaldii Leloup 1933		4(1)			7	1.3	Upper 100 m
L. hotspur Totton 1954	1273(11)	855(35)	1711(31)		5	0.9	Upper 100 m to surface
L. meteori Leloup 1934			14(1)		5		Upper 100 m
L. multicristata Moser 1925	61(4)	730(36)	498(23)		17	3.5	Upper 100 m and depth
L. subtilis Chun 1886			115(3)		12	2.2	Surface
L. subtiloides (Lens and Van Riemsdijk) 1908			31(2)		5	1	Surface
Chuniphyes multidentata Lens and van Riemsdijk 1908	2(1)	4(1)	37(2)		40	7.6	Upper 100 m and depth
Sulculeolaria biloba Sars 1846		12(2)	29(2)		20	4	Surface and depth
S. chuni Lens and van Riemsdijk 1908	34(1)	3(1)	113(4)		8	1.5	Upper 100 m

TABLE 1 (CONTINUED)

Abundance of Predatory Species (Frequency, in Parentheses) with Information on Size and Depth Distribution.[1]

Species	Total number (and frequency) 1954 (849 hauls)	1956 (316 hauls)	1958 (899 hauls)	~ Maximum size (mm)	Nect.	cm complete animal	Depth distribution
S. monoica Chun 1888	94(1)	45(6)	94(7)		10	2	Surface and depth
S. quadrivalvis Blainville 1834	86(4)	65(7)	796(29)		20	3.7	Upper 100 m to surface
Abyla bicarinata Moser 1925		6(2)			10	2	Upper 100 m
A. brownia Sears 1953		41(2)					Upper 100 m to surface
A. haeckeli Lens and van Riemsdijk 1908		9(2)	53(7)		9	1.8	Upper 100 m to surface
Abylopsis eschscholtzi Huxley 1859			26(3)		8	1.3	Upper 100 m to surface
A. tetragona Otto 1823	165(3)	3(1)	3(1)		20	4.3	Upper 100 m to surface
Bassia bassensis Quoy and Gaimard 1834		92(2)	88(2)		7	1.3	Upper 100 m to surface
Velella velella Linne 1758		4(2)				10.4	Surface
					μm (height ×width)		
Euphysora furcata Kramp 1948	6(1)		13(3)		8×6.5		Surface
Annatiara affinis (Hartlaub) 1913		3(1)			23		Upper 100 m during upwelling
Leuckartiara octona (Fleming) 1823			82(4)		20		Upper 100 m to surface
L. zacae Bigelow 1940	840(32)	326(36)	806(22)		21×18		Upper 100 m to surface
Octotiara russelli Kramp 1953		3(1)			7		Surface
Bythotiara murrayi Gunther 1903		3(1)			20		Upper 100 m during upwelling
Calycopsis nematophora Bigelow 1913		2(1)			30		Upper 100 m to surface
C. simulans (Bigelow) 1903			52(1)		30×22		Upper 100 m to surface
Sibogita geometrica Maas 1905	7(1)				38×20		Upper 100 m
Melicertum georgicum Agassiz 1862			7300(1)		20		Upper 100 m to surface
Mitrocoma discoidea Torrey 1909	10(1)				45		Surface
Obelia spp.	6(1)	147(3)			6		Upper 100 m to surface
Phialidium gregarium (L. Agassiz) 1862	97(2)				12		Surface
Eirene hexanemalis (Goette) 1886			3(1)		18		Surface
Phialopsis diegensis Torrey 1909	655(13)	78(12)	153(8)		10×30		Upper 100 m
Gossea brachymera Bigelow 1909			21(3)		20		Surface
Liriope tetraphylla (Chamisso and Eysenhardt) 1821	39853(119)	16035(148)	21548(99)		30		Upper 100 m to surface
Aglaura hemistoma Pèron and Lesueur 1809	3892(14)	3157(11)	33144(58)		6×4		Upper 100 m to surface
Colobonema sericeum Vanhoffen 1902			11(1)		45×35		Upper 100 m and deep waters
Rhopalonema velatum Gegenbaur 1856	5709(57)	2883(60)	9913(78)		10		Upper 100 m to surface
Aegina citrea Eschscholtz 1829	134(50	1032(17)	82(3)		50		Surface and deep water
Aeginura beebei Bigelow 1940			3(1)		18×100		Upper 100 m
A. grimaldii Maas 1904	186(5)	329(9)	225(9)		45		Upper 100 m and deep water
Solmundella bitentaculata (Quoy and (Gaimard) 1822		240(4)	9(1)		12		Upper 100 m to surface
Pegantha clara R.P. Bigelow 1909		14(2)	6(1)		25×55		Upper 100 m
P. laevis H.B. Bigelow 1909		3(1)			40		Upper 100 m
Solmaris corona (Keferstein and Ehlers)1861	8(2)	108(8)			>15		Upper 100 m and surface
S. rhodoloma (Brandt) 1838	13800(1)				7		Surface
Cunina globosa Eschscholtz 1829		6(1)			18		Surface
C. tenella (Bigelow) 1909		3(1)			7		Surface
Atolla wyvillei Haeckel 1880			6(2)		150		Upper 100 m during upwelling
Atorella vanhoeffeni Bigelow 1909		7(2)			7		Upper 100 m during upwelling
Periphylla periphylla (Pèron and Lesueur) 1809	3(1)		4(1)		200		Upper 100 m during upwelling
Pelagia colorata Russell 1964		2(1)			450		Surface
Bolinopsis sp.		10(2)	116(1)		122		Surface
Pleurobrachia sp.	182(2)	765(2)	121(1)		30, tentacles 20 times longer		Surface
Mertensia ovuum (Fabricius) 1780		3(1)			55, tentacles 5 times longer		Surface
Beroe sp.	1397(55)	443(44)	632(29)		>90		Surface

[1] Size and depth distribution from Alvariño unpublished and published information.

siphonophores, chondrophores, medusæ, and ctenophores in the California Current is not available elsewhere.

Chaetognatha

Altogether 22 species of Chætognatha were observed in the collections analyzed. Not all of the species were taken in a given year; rather, 17 species were found in 1954 collections, 16 in 1956, and 18 in 1958. Only 12 species were taken in all three years. The species occurring in greatest abundance were *Sagitta euneritica* (maximum size 15.5 mm), *S. bierii* (maximum size 17 mm), and *S. enflata* (maximum size 25-30 mm). Of these, *S. enflata* is the most voracious predator of fish larvae. The size of chætognaths obtained ranged from 6 to more than

90 mm in length. The predatory potential of an individual chætognath is roughly proportional to its size; the predatory potential of the species is related to both size and abundance.

Siphonophorae

During the three years, 48 species of siphonophores were observed, with the largest complement of species; 40 taken in 1956, 37 in 1958, and only 26 in 1954. Specimens of siphonophores ranged in size from 5 mm total length for nectophores of some species of Diphyidæ in the polygastric phase, to several meters in total length in various species of Agalmidæ and related families. Undoubtedly, the siphonophores in the family Agalmidæ are among the most successful predators inasmuch as they can move swiftly through the waters and can act as living nets in capturing other plankters. The only commonly occurring agalmid in CalCOFI collections was *Stephanomia bijuga*; this could be one of the primary predators on fish larvae. Several siphonophores in the family Diphyidæ are common to abundant, including *Chelophyes appendiculata, Muggiaea atlantica, Lensia challengeri, L. hotspur,* and *Diphyes dispar.* The latter species was commonly taken only in 1954; among diphyid siphonophores it is a relatively large species, consequently it has the potential to be an effective predator on fish larvae. *M. atlantica*, the most abundant diphyid, particularly in inshore waters, is a small species that would be an effective predator only on small anchovy larvae. *C. appendiculata*, also among the most common diphyid siphonophores, is large, hence perhaps a more effective predator on fish larvae.

Chondrophorae

Only a single species was observed, *Velella velella,* and this only in two hauls made in 1956.

Medusae

The total number of species of Medusæ taken during the three years was 34, with 15 species in 1954, 20 in 1956, and 19 in 1958. The distribution of Medusæ is more erratic than that of Chætognatha or Siphonophoræ. Only seven species were common to the three years; of these the most abundant species, both with regard to abundance and to frequency of occurrence, were *Liriope tetraphylla* and *Rhopalonema velatum*.

Ctenophora

Ctenophores except *Beroë* sp. were infrequently taken. Although there were 128 occurrences of *Beroë* sp. recorded during the three years, there were only five occurrences of *Pleurobrachia* sp., three of *Bolinopsis* sp., and one of *Mertensia ovum*. Even so, the number of specimens of *Pleurobrachia* or *Bolinopsis* in the samples in which they did occur could be quite large (i.e. over 100 individuals per sample). Most ctenophores occur at or near the surface; hence, their predation would be limited to this zone. *Beroë* is known to feed on other Ctenophora, but the other ctenphores are known to be voracious predators on zooplankton including fish larvae (Chun 1880; Kamshilov 1960; Kamshilov et al. 1958; Horridge 1965; Lebour 1922, 1923; Mayer 1912; Miller 1974; Swanberg 1974). As mentioned earlier, Ctenophora tend to fragment and disintegrate on preservation and could easily be overlooked.

ABUNDANCE OF THREE GROUPS OF PREDATORS IN RELATION TO ABUNDANCE OF ANCHOVY LARVAE

Variations in the composition of species of all groups were observed in all years. Tropical species were taken in 1958, the year with warmer than average temperatures. The highest variability occurred in the Medusæ, which show erratic distribution both in time and space.

Information on the abundance of Chætognatha, Siphonophoræ, and Medusæ is summarized for 3-month intervals for the three years, 1954, 1956, and 1958, in Table 2. Yearly abundance values are summarized in Table 3 and illustrated in Figure 1.

Monthly average abundance of plankton predators are compared to the monthly percentage concentration of anchovy larvae (from Ahlstrom 1967) for all three years in Figure 2.

Chaetognatha

Little or no relation appeared between abundance of anchovy larvae and abundance of chætognaths. This applies both for abundance of total chætognaths versus anchovy larvae and for *Sagitta enflata*, a common species known to be a prime predator on fish larvae. The only prime predator species to show an inverse abundance relation with anchovy larvae, i.e. fewer present when anchovy larvae were abundant, was *Sagitta hexaptera*. However, it should be noted that the two most abundant chætognaths, *S. euneritica* and *S. bierii* are not considered important predators on fish larvae, because of their size, and the abundance is mainly made up of young specimens, too small to feed on anchovy larvae.

Siphonophorae

During two of the three years, 1954 and 1958, lowest abundance of siphonophores occurred in hauls with high abundance (> 241/haul) of anchovy larvae. The inverse relation was most marked in the warmest year, 1958, when only 12 siphonophores/1,000 m^3 on the average were taken in hauls with anchovy larvae counts exceeding 241 larvae/standard haul, 33 siphonophores/haul on the average for low abundance of anchovy larvae (1 to 241/standard haul), and 101 siphonophores in hauls with 0 anchovy larvae.

However, in 1956, siphonophores were more abun-

TABLE 2

Part I. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with High Number of Anchovy Larvae (i.e. > 241 Larvae per Standard Haul) in 1954, 1956, 1958.

	Predators	Chaetognatha			Siphonophorae			Medusae			Average all categories
Cruises	Number hauls	Number species	Total count	Average count	Number species	Total count	Average count	Number species	Total count	Average count	
5401-5403	41	12	139,906	3,412	8	2,024	49	3	175	4	3,465
5404-5406	22	11	116,767	5,308	4	319	14	3	56	3	5,378
5407	3	4	24,304	8,101	2	28	9	3	153	51	8,161
5412	3	5	12,522	4,174	1	25	8	0	0	0	4,182
Yearly total	69	13	293,499	4,254	9	2,396	35	4	384	6	4,295
5601-5603	15	12	35,869	2,391	11	2,093	140	5	930	62	2,593
5604-5606	18	7	66,909	3,717	8	5,042	280	4	872	48	4,045
5607-5608	8	7	15,228	1,904	4	1,741	218	1	1,035	129	2,251
5610-5612	–	–			–			–			–
Yearly total	41	12	118,006	2,878	15	8,876	216	6	2,837	69	3,163
5801-5803	53	15	149,975	2,830	8	652	12	7	151	3	2,845
5804-5806	48	13	409,398	8,529	8	536	11	4	103	2	8,542
5807	4	7	35,522	8,888	2	31	8	0	0	0	8,896
5810-5812	–	–			–			–			–
Yearly total	105	16	594,895	5,666	12	1,219	12	9	254	2	5,680

Part 2. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with Low Concentration of Anchovy Larvae (i.e. 1 to 241 Specimens per Standard Haul) in 1954, 1956, 1958.

Cruises	Number hauls	Number species	Total count	Average count	Number species	Total count	Average count	Number species	Total count	Average count	Average all categories
5401-5403	91	14	206,977	2,274	10	14,525	159	4	986	10	2,443
5404-5406	135	14	741,944	5,495	16	18,025	133	8	11,622	86	5,714
5407-5409	74	13	745,777	10,078	8	3,508	47	8	4,761	64	10,189
5410-5412	34	13	110,430	3,259	8	1,693	49	5	2,721	80	3,388
Yearly total	334	16	1,805,128	5,405	23	37,751	113	12	20,090	60	5,578
5601-5603	57	14	253,326	4,444	17	8,321	146	9	1,482	26	4,616
5604-5606	39	9	115,795	2,969	10	6,381	163	5	3,220	82	3,214
5607-5608	20	12	60,705	3,035	12	6,642	332	6	2,128	106	3,475
5610-5612	10	10	25,121	2,512	10	1,664	166	2	968	96	2,774
Yearly total	126	14	454,947	3,611	24	23,008	183	11	7,798	62	3,856
5801-5803	116	13	474,664	4,091	20	3,883	33	8	1,755	15	4,139
5804-5806	143	16	682,198	4,770	17	5,390	37	8	2,774	19	4,826
5807	26	10	126,351	4,859	6	214	8	2	634	24	4,891
5810-5812	13	15	33,753	2,596	3	312	24	3	303	23	2,643
Yearly totaL	298	17	1,316,966	4,419	25	9,799	33	11	5,466	18	4,470

Part 3. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with Absence of Anchovy Larvae in 1954, 1956, 1958.

Cruises	Number hauls	Number species	Total count	Average count	Number species	Total count	Average count	Number species	Total count	Average count	Average all categories
5401-5403	94	17	238,679	2,539	13	9,075	97	4	2,490	26	2,662
5404-5406	210	15	592,525	2,822	16	17,253	82	6	19,512	93	2,997
5407-5408	75	13	449,014	5,986	9	6,760	90	7	5,076	68	6,144
5410-5412	67	16	217,842	3,251	10	6,386	95	6	17,654	263	3,609
Yearly total	446	17	1,498,060	3,359	21	39,474	89	10	44,732	100	3,548
5601-5603	46	12	113,954	2,477	28	5,606	122	8	5,389	117	2,716
5604-5606	44	14	75,215	1,709	20	11,939	271	11	4,570	104	2,084
5607-5609	26	13	131,240	5,048	15	9,049	348	9	1,632	63	5,459
5610-5612	33	13	59,742	1,810	18	1,805	55	9	2,155	65	1,930
Yearly total	149	15	380,151	2,551	37	28,399	191	17	13,746	92	2,834
5801-5803	129	18	241,677	1,873	22	11,374	88	10	4,186	32	1,993
5804-5806	211	16	436,361	2,068	29	30,844	146	11	42,592	201	2,415
5807	55	12	80,724	1,467	15	3,734	67	5	8,899	161	1,695
5810	101	16	133,053	1,317	12	4,116	40	4	11,984	118	1,475
Yearly total	496	18	891,815	1,798	32	50,068	101	14	67,661	136	2,035

dant in all types of hauls than in the other two years and were equally abundant in hauls with > 241 anchovy, < 241 anchovy larvae, and 0 anchovy larvae.

One of the siphonophores that is probably an effective predator on fish larvae is the diphyid *Chelophyes appendiculata*. This species had a striking inverse relation to abundance of anchovy in all three years. Another diphyid species, *Diphyes dispar*, was commonly taken only in

TABLE 3

Yearly Abundance of Chaetognatha, Siphonophorae, and Medusae in the Three Categories of Anchovy Hauls: High, Low, and Zero Abundance.

Anchovy abundance	Number hauls	Chaetognatha			Siphonophorae			Medusae			Average count 3 plankters
		Number species	Total specimens	Average count/haul	Number species	Total specimens	Average count/haul	Number species	Total specimens	Average count/haul	
1954											
High, > 241	69	13	293,499	4,254	9	2,396	35	4	384	6	4,295
Low, < 241	334	16	1,805,128	5,405	23	37,751	113	12	20,090	60	5,578
Zero anchovy	446	17	1,498,060	3,359	21	39,474	89	10	44,732	100	3,548
1956											
High, >241	41	12	118,006	2,878	15	8,876	216	6	2,837	69	3,163
Low, < 241	126	14	454,947	3,611	24	23,008	183	11	7,798	62	3,856
Zero anchovy	149	15	380,151	2,551	37	28,399	191	17	13,746	92	2,834
1958											
High, > 241	105	16	594,895	5,666	12	1,219	12	9	254	2	5,680
Low, < 241	298	17	1,316,966	4,419	25	9,799	33	11	5,463	18	4,470
Zero Anchovy	496	18	891,815	1,798	32	50,068	101	14	67,661	136	2,035

1954; in fact, 96.3% of the total specimens of this species were obtained during this year, 3% in 1956, and less than 1% in 1958. In the 1954 collections, there was also a marked inverse relation between abundance of this species and of anchovy larvae. The agalmid, *Stephanomia bijuga*, was the only one in this family taken in any abundance; it was least common in hauls containing high counts of anchovy larvae.

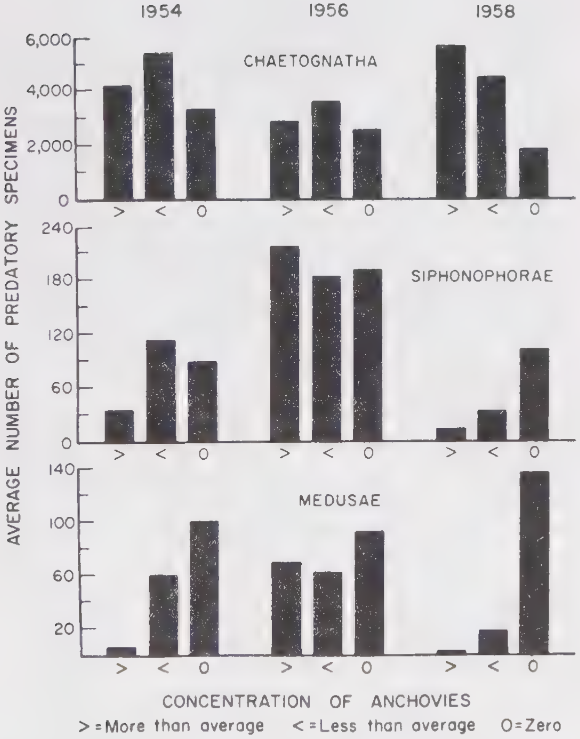


Figure 1. Yearly abundance of predators (Chætognatha, Siphonophoræ, Medusæ) and concentration of anchovy larvæ (high = more than 241 larvæ per standard haul, low = less than 241 anchovy larvæ per standard haul, zero = absence of anchovy larvæ).

Medusae

During 1954 and 1958, abundance of medusæ showed a striking inverse relation with abundance of anchovy larvae. However, as also shown above for siphonophores, this relation breaks down in 1956. In this year, one species of medusæ, *Liriope tetraphylla*, contributed 85% of the specimens of medusæ in hauls with high anchovy counts, 74% in hauls with low anchovy counts, and 67% in zero count hauls. This is a moderately large species attaining a width across the umbrella of 30 mm, hence undoubtedly an effective predator on fish larvae.

RELATION OF UPWELLING AND ANCHOVY LARVAE

Sagitta decipiens has been used as an indicator of upwelling (Alvariño 1965; Nair 1977; Nair and Rao 1973; and others). During the three years studied, *S. decipiens* was taken in 93 of 2064 hauls, or in 4.5% of the hauls. During 1954 it was taken in only 12 hauls, or in 1.4%; in 1956 it was taken in 35 hauls or in 11.1% of the hauls; in 1958 it was taken in 46 hauls or in 5.1% of the hauls.

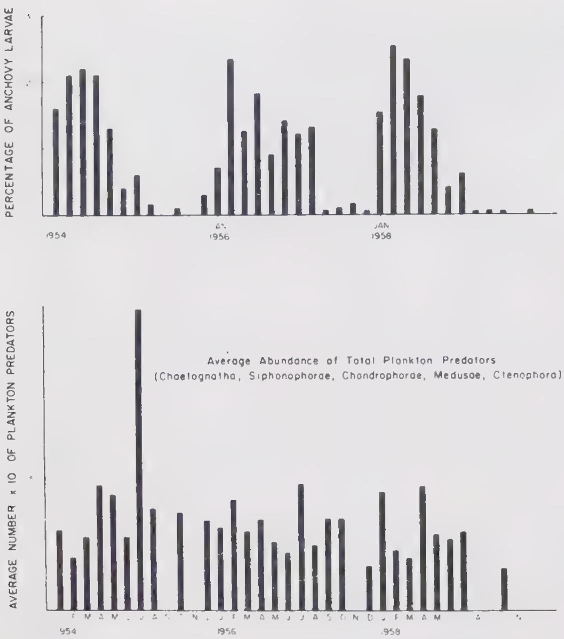


Figure 2. Monthly average of abundance of plankton predators, compared with Ahlstrom (1967) monthly percentages of anchovy larvæ for 1954, 1956, and 1958.

Hence, based on *S. decipiens* as an indicator of upwelling, this phenomenon was most intense in 1956, intermediate in 1958, and low in 1954, which agrees with Bakun (1973) and Wyllie (1966). Occurrences are probably preferable to actual counts of specimens because of the influence on counts of few large hauls. In fact, 36.2% of the total specimens taken in all three years were obtained at a single station in April of 1954. This may have been an indication of intense upwelling at that station, but it certainly biases results based on counts. Based on numbers taken, the average abundance per haul was 10.0 in 1956, 4.1 in 1954, and 1.9 in 1958. However, for stations other than that in 5404, the average count per haul was 0.5 specimens for 1954.

Sagitta decipiens occurred in 2.8% of the hauls with large concentrations of anchovy larvae, in 4.35 % of the hauls with low counts of anchovy larvae, and in 4.95% of the hauls with zero anchovy abundance. This could be interpreted as an indication that large concentrations of anchovy larvae occur infrequently in upwelling areas.

Based on occurrence by quarters (seasons) of the year, there were 3.6% positive hauls in winter, 4.5% in spring, 4.1% in summer, and 6.1% in the fall. Occurrences in 1956 contributed substantially to the fall total, inasmuch as 11 of 43 hauls taken in these months in 1956 contained *Sagitta decipiens* (i.e. it occurred in over 25% of the hauls). This appears to be the period of most widespread upwelling encountered during the three years. During 1958, upwelling as indicated by the occurrences of *S. decipiens* was most widespread during the spring months.

RELATION OF PLANKTON ASSEMBLAGES TO ANCHOVY LARVAE

To obtain information on the plankton assemblages associated with high and zero abundance of anchovy larvae, several stations with high and zero abundances of anchovy larvae were selected from each monthly cruise within the main anchovy spawning areas. The number of stations thus chosen from 1954 survey cruises was 27 with high anchovy abundance and 33 with zero anchovy abundance; for 1956 the number of corresponding stations was 30 and 36, and for 1958, it was 19 and 33.

During 1954, 14 of the 27 stations with high concentrations of anchovy larvae were dominated by copepods, 11 by copepods and euphausiids, and 2 by euphausiids and pteropods. In contrast, 17 of the 33 stations with zero abundance of anchovy larvae contained predominantly salps; 4 stations were dominated by salps and doliolids; 4 others were mostly decapod larvae; 1 each were dominated by pteropods, by heteropods, by polychætes, by euphausiids, and by euphausiids and decapods; and the other 3 had a mixture of constituent organisms.

During 1956, 22 of the 30 collections from stations with high abundance of anchovy larvae were dominated by copepods, 5 by copepods and euphausiids, 2 by euphausiids, and 1 by copepods, euphausiids, and pteropods. The selected stations from 1956 that lacked anchovy larvae had 23 of 36 composed mostly by pyrosomes; 1 had a mixture of pyrosomes and salps; 3 contained mainly salps; 4 were dominated by megalopa larvae; 2 included mostly pyrosomes and the euphausiid *Euphausia pacifica*, and 1 had salps with *E. pacifica*; and 2 had a mixture of constituents. Pyrosomes were markedly more abundant in 1956 than in the other two years.

During 1958, 16 of the 19 collections from stations with high counts of anchovy larvae were dominated by copepods, and 1 each with copepods and euphausiids, with copepods and pteropods, and with a mixture of constituents. The dominant constituents of the 33 stations that lacked anchovy larvae were salps in 16, megalopa larvae in 2, doliolids in 1, doliolids and salps in 1, pteropods in 1, copepods in 1, and a miscellaneous array of constituents without a dominant group in 11.

The dominant plankton constituents in hauls with large concentrations of anchovy larvae were markedly different from the constituents in hauls with zero anchovy larvae (Figure 3). In the former, the dominant constituents in most hauls were copepods, followed by euphausiids alone or copepods and euphausiids, and less frequently with pteropods together with euphausiids and/or copepods.

Areas in which these constituents dominate could be called "anchovy water." Hauls from areas lacking anchovy had only an occasional sample with copepods or euphausiids as the dominant constituent, and the majority of the samples were dominated by jelly-like organisms, by salps, or salps and doliolids in 1954 and 1958 and by pyrosomes in 1956. In "anchovy water," the organisms needed for food for anchovy larvae, particularly copepods, were abundant. In areas lacking anchovy larvae, organisms needed for food by anchovy larvae were scarce.

Most Abundant Large Predators and High and Zero Concentration of Anchovy Larvae

Invertebrate predators in the three main groups (Chætognatha, Siphonophoræ, and Medusæ) were present in many of the hauls containing large numbers of anchovy larvae, as well as in the hauls lacking anchovy larvae during these three years, 1954, 1956, and 1958. In fact, two species, the chætognath, *Sagitta euneritica*, and the siphonophore, *Muggiaea atlantica*, occurred in larger numbers in anchovy-rich hauls than in hauls lacking anchovy larvae. Both species are small in size. Abundance of *S. euneritica* is usually contributed by young specimens, not observed to prey on anchovy larvae.

The species considered to have the highest potential as predators because of size and abundance are the chætognaths, *Sagitta enflata*, *S. hexaptera*, and *S. scrippsae*; the siphonophores, *Stephanomia bijuga, Chelophyes appendiculata*, and *Diphyes dispar*; and the medusæ *Liriope tetraphylla*, *Rhopalonema velatum*, and *Aglaura hemistoma*, (Table 4). These species are present in fewer of the anchovy-rich hauls in all instances and occur in lesser abundance in most comparisons (i.e. 18 out of 21).

The species showing the greatest difference between anchovy-rich and anchovy-lacking stations are *Sagitta hexaptera, Chelophyes appendiculata, Rhopalonema velatum,* and *Aglaura hemistoma*. *S. hexaptera* occurred twice as often in hauls lacking anchovy larvae as in anchovy-rich hauls, and for the other three species the disproportion between occurrences and numbers in anchovy-lacking versus anchovy-rich hauls is even more marked. The siphonophore, *Stephanomia bijuga*, also occurred most frequently and in large numbers in hauls lacking anchovy rather than in anchovy-rich hauls in all three years.

Although the medusa, *Liriope tertaphylla*, and markedly more abundant in hauls lacking anchovy larvae in 1954 and 1958 than in anchovy-rich hauls, it was present in about the same percentage of hauls of the two categories in 1956 and was more abundant on the average in anchovy-rich hauls during that year. As noted previously, the siphonophore *Diphyes dispar* was commonly taken during 1954, when it occurred more frequently and in larger numbers in collections lacking anchovy larvae. The other two chætognaths were taken in greater abundance in anchovy-rich hauls than in hauls lacking anchovy larvae in one of the three years, in 1956 for *Sagitta enflata* and in 1954 of *S. scrippsae*, but even for these the frequency of occurrences was higher in hauls lacking anchovy larvae in all three years.

SUMMARY

In summary, the numbers and kinds of plankton carnivores, potential predators on fish larvae, have been studied for five groups, Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora, for three CalCOFI years, 1954, 1956, and 1958. Altogether, 22 species of Chætognatha, 48 species of Siphonophoræ, 1 Chondrophoræ, 34 Medusæ, and 5 Ctenophora were recorded. For each of these species, abundance and number of occurrences are given in Table 1 for each of the years.

Collections studied could be grouped into three categories with respect to anchovy larvae: anchovy rich (more than 241 larvae per standard haul), anchovy poor (1 to

TABLE 4

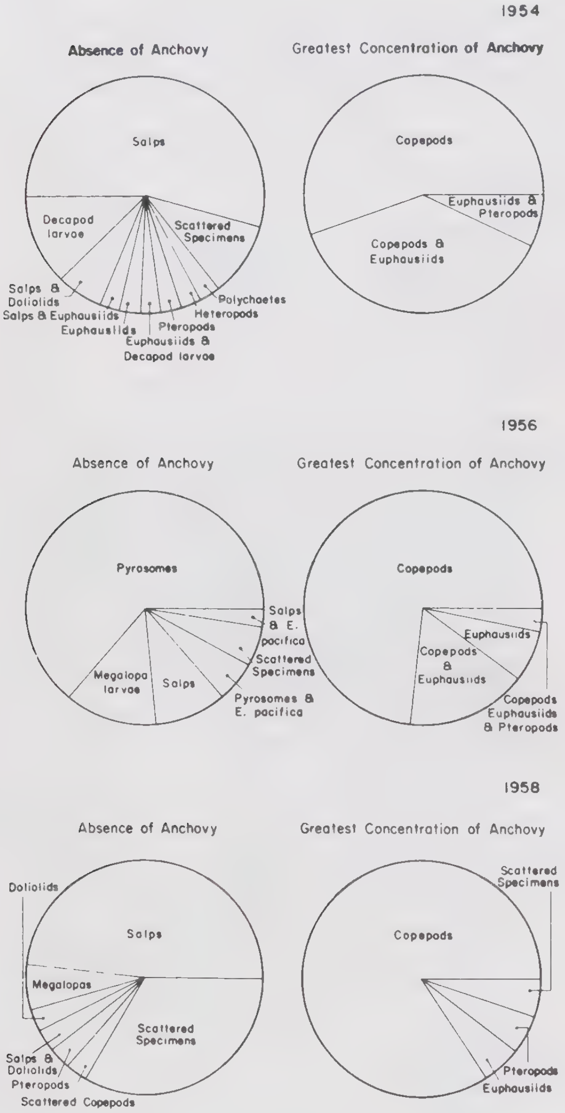
Most Abundant Large Species of Predators Occurring with the Highest and with Zero Concentrations of Anchovy Larvae.

Anchovy larvae abundance	1954				1956				1958			
	High		Zero		High		Zero		High		Zero	
Sps. abundance Species	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.
Sagitta enflata	56	491.3	73	1,093.7	43	191.8	47	121.6	74	271.6	82	308.4
S. hexaptera	22	5.5	55	16.1	27	1.8	53	62.0	26	15.5	52	42.2
S. scrippsae	33	48.1	52	19.2	20	3.2	33	17.4	16	6.5	27	9.9
Stephanomia bijuga	7	0.2	27	0.8	13	1.2	22	2.0	11	0.2	27	1.8
Chelophyes appendiculata	33	10.0	76	89.3	17	5.0	47	7.6	32	2.6	67	46.2
Diphyes dispar	22	14.7	48	44.1	0	0	0	0	0	0	3	0.4
Liriope tetraphylla	22	20.9	64	253.6	37	96.5	42	41.8	21	6.8	58	89.4
Rhopalonema velatum	7	0.6	46	30.3	7	0.3	28	4.1	5	0.3	33	18.2
Aglaura hemistoma	0	0	12	40.2	0	0	3	1.1	5	0.2	18	51.7

[1] Average from all localities occupied, including those where species were present and absent.

240 larvae per standard haul), and anchovy lacking (zero anchovy larvae per standard haul). An inverse relation between abundance of anchovy larvae and abundance of predators was found for most siphonophores and medusæ, but the relation numerically is less well defined for chætognaths.

An unanticipated finding was that anchovy larvae occur in abundance primarily in hauls dominated by Copepoda and/or Euphausiidæ and never in hauls dominated by pelagic prochordates (salps or pyrosomes). The habitat of the former association can be characterized as "anchovy water."



In the introduction it was pointed out that the major causes of larval mortality are starvation and predation and that these may interact. This investigation, which studied the distribution and abundance of predatory and other planktonic organisms in relation to abundance of anchovy larvae, helps to confirm that statement.

One of the characteristics of "anchovy water" is the presence of potential food for anchovy larvae in some abundance. Another characteristic is that potential predators among chætognaths, siphonophores, and medusæ occur usually in lesser abundance than in hauls lacking anchovy larvae. In anchovy waters these potential predators have a greater range of prey to feed upon and, as evidenced by gut contents, prey primarily on copepods.

The best way to reduce mortality from starvation is for the anchovy larvae to be in waters with an adequate food supply. The best way to reduce mortality from predation is for anchovy larvae to be in waters where potential predators are in reduced abundance. This favorable combination of factors has been shown for "anchovy water."

ACKNOWLEDGMENTS

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REPRODUCTION SEASONS AND DAY/NIGHT BATHYMETRIC DISTRIBUTION OF THREE SPECIES OF DIPHYINAE (SIPHONOPHORAE), OFF CALIFORNIA AND BAJA CALIFORNIA

ANGELES ALVARIÑO

INTRODUCTION

Muggiaea atlantica, Chelophyes appendiculata and *Eudoxoides spiralis* are abundant off California and Baja California. Published works [1,2,3,4,5,6,7,8,9] included information on the species, and in [7] are studies as predators of *Engraulis mordax* larvae. Previous works [10,11] on day/night bathymetric distribution are not based on continuous series of hauls at same locations and depths, and no works are available on polygastric and eudoxid stages through the seasons.

MATERIALS AND METHODS

Plankton analyzed were seasonal cruises of 1969 California Cooperative Oceanic Fisheries Investigations (CalCOFI). for winter (Feb-Mar, 6902-03), spring (May-June, 6905-06), summer (Aug-Sep, 6908-09), fall (Nov-Dec, 6911-12). Paired open-closing bongo nets were used in oblique hauls, calibrated by speed and length of stratum to strain $1000m^3$ of water. Sampling covered CalCOFI region grid (stations on lines 70, 90, 120), roughly off Monterey, San Diego, Punta Eugenia; with tows at each station and depth stratum around noon and midnight (about 12 hours time difference at same location and depth from daylight to night hauls). Strata sampled: 600-475m, 475-350m, 350-225m, 225-100m, 100-75m, 75-50m, 50-25m, 25-0m depth.

The entire plankton samples from both paired nets were examined from each haul. No fraction of samples was taken.

Physico-chemical data obtained during the cruises are used in the discussion.

Standardization of counts of specimens in strata above and below 100-m layer to quantitatively compare data to $1000m^3$ water for each 25-m depth, was obtained by the formula: $N = n \frac{(\text{opening depth-closing depth})}{25}$

N = standardized number of specimens

n = number of specimens counted in both paired nets.

The difficulty in quantitative determination of siphonophores was solved in Diphyinae by counting superior and inferior nectophores, bracts and gonophores, and the highest number of either part was applied to the respective polygastric and eudoxid population.

RESULTS

Muggiaea atlantica Cunningham 1892, *Chelophyes appendiculata* Eschscholtz 1829, *Eudoxoides spiralis* Bigelow 1911, are the most abundant siphonophores, together with some species of *Lensia*, in the California and Baja California regions.

M. atlantica inhabits neritic waters of those regions. Polygastric stages extended from 0 to 225 m in winter, spring and summer, and to 100m in the fall. Highest abundance of eudoxids was at upper 75 m in winter and 50 upper m in spring, and absent in summer and fall, probably due to development of benthic stage, as stated[12] for *M. kochi* (closest related to *M. atlantica*) (Table 1).

Polygastric population obtained at daylight was 5 times that at night, and daylight eudoxid population was more than 12 times that obtained at night.

Reproduction may occur late in winter and spring.

M. atlantica inhabited layers above thermocline, and greatest concentrations occurred at 32.98-34.0 ‰ salinity, 9.0°C-20.99°C temperature, and 4.38-6.1 ml/L oxygen.

Ch. appendiculata, the most abundant siphonophore in these regions, was present in all stations covered by 1969 cruises. It was more abundant off San Diego and Punta Eugenia than off Monterey. Polygastric population peaks were respectively at daylight and night, at 0-25m, 50-75m in winter and fall, and 0-25m and 25-50m in spring and summer. Polygastric population was more abundant in daylight hauls of spring, followed by day/night hauls of summer, fall and winter.

Eudoxid population presented peaks at 0-25 and 50-75m depth, respectively, at daylight and night, in winter and spring, and in summer and fall were scattered through the depth strata.

Daylight average abundance of polygastric population was about 1.2 of night, and daylight eudoxid population was 20 times that of night. Polygastric and eudoxid populations were highest in spring. Polygastric population was lowest in winter, and eudoxid population in the fall. Reproduction appears to be continuous through the seasons, with peaks in spring and summer (Table 2).

Highest concentration of *Ch. appendiculata* occurred at 32.22-33.67 ‰ salinity, 9.14-20.75°C temperature, and 4.38-6.2 ml/L oxygen. It was found at the thermocline and above and below this structure.

Day/night changes did not agree with [10,11].

E. spiralis was mainly abundant in warm waters of southernmost and offshore locations under the influence of warm currents. Polygastric population was highest in winter, followed by summer and fall, with minima in spring. Eudoxids started to increase in winter, with a peak in spring, diminishing through summer and fall. Polygastric and eudoxid populations marked the rhythm of alternation of generations, maximum polygastric of winter was followed by maximum eudoxid of spring, which may be responsible for the increase of summer polygastric population. Reproduction appears continuous through the year. Polygastric population was more abundant in daylight hauls of winter, summer and fall, and night hauls of spring. Eudoxid population was more abundant at uppermost layers during night hauls of winter, and daylight hauls of spring, summer and fall (Table 3).

Daylight polygastric population was 1.2 of the night population. The eudoxids collected at daylight were 4 times those at night.

Maximum concentration of *E. spiralis* concurred with 32.8-34.01 ‰ salinity, 13.1-20.75°C temperature, 5.2-6.3 ml/L oxygen. It was mainly present above the thermocline.

The total polygastric population of *M. atlantica* during 1969 was 35,815 specimens, an average of 78 per haul, and the eudoxid population amounted to 6,260 (average of 13 specimens per haul). Total polygastric population of *Ch. appendiculata* was 16,897 (average of 37 specimens per haul), and the euxoxid population was 9,327 specimens (average of 20 per haul). Total polygastric population of *E. spiralis* was 8,888 (19 specimens per haul), and 17,864 eudoxids (average of 39 per haul).

Highest concentrations of polygastric and eudoxids occurred always during daylight hauls, for *M. atlantica* in winter, *Ch. appendiculata* in spring, and *E. spiralis* in winter and spring, respectively.

These species are active predators on fish larvae and found[7] inversely related to concentrations of anchovy larvae. *M. atlantica* was abundant in "anchovy water"[7], rich in small calanoid copepods, and in 1969 was also present with anchovy larvae.

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Table 1. Seasonal day/night bathymetric distribution of *Muggiaea atlantica* (polygastric and eudoxid stages) during 1969.

Sta.	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Total Average			
																							Day		Night	
Depth	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Poly.	Eudox.	Poly.	Eudox.
6902-03																										
25- 0	0	0	17	0	-	-	-	-	638 + 3335*	0	508 + 31*	16 + 16*	-	-	14978	94	617	211	8	0	0	0	2095	420	40	2
50- 25	-	0	0	0	-	-	-	-	165 + 510*	0 + 36*	790 + 1231*	0	-	-	2404	392	-	98	0	8	0	0	559	600	62	4
75- 50	20	-	0	-	-	-	-	-	0	148 + 48*	51 + 273*	0	-	-	31	0	-	98	0	0	-	-	17	45	49	9
100- 75	16	-	0	-	-	-	-	-	0	140	51	0	-	-	78	156	7	0	0	0	0	0	12	0	49	0
225-100	-	-	0	-	-	-	-	-	0	-	0	-	-	-	11	-	-	0	-	0	0	0	2	0	0	0
350-225	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	0	-	-
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
																							2685	1065	191	15
															Polygastric average D/N total: 2776/2 =							1388				
															Eudoxid average D/N total: 1080/2 =							540				
6905-06																										
25- 0	1	0	50	0	0	4	0	0	-	76 + 740*	0	0	0	0	0	0	70	0	430	0	0	0	60	0	7	67
50- 25	0	2	6	0	0	0	-	0	-	0 + 40*	0	0	0	0	0	42	1	44	456	0	-	0	66	0	8	3
75- 50	8	0	10	0	0	0	-	0	-	0	18	0	16	0	0	0	0	75	27	0	0	0	8	0	6	0
100- 75	0	0	0	0	0	0	-	0	-	0	1	0	-	0	0	0	-	5	-	0	-	0	0.2	0	0.4	0
225-100	0	0	0	0	0	0	0	0	-	40	0	0	-	0	0	0	96	0	0	0	-	0	12	0	3	0
350-225	-	0	0	0	0	0	0	0	-	0	0	0	-	-	0	0	0	0	0	-	-	0	0	0	0	0
475-350	0	0	0	0	0	0	0	0	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
600-475	0	0	0	0	0	0	-	0	-	0	0	0	-	0	0	0	0	-	0	0	-	0	0	0	0	0
																							146	0	24	70
															Polygastric average D/N total: 170/2 =							85				
															Eudoxid average D/N total: 70/2 =							35				
6908-09																										
25- 0	-	-	-	1022	-	82	-	2	0	0	184	0	0	0	510	90	0	0	30	0	0	0	103	0	119	0
50- 25	-	-	-	117	1944	82	18	196	0	0	66	0	0	0	225	1005	-	0	0	0	0	0	281	0	140	0
75- 50	-	-	-	0	1863	138	191	308	90	0	-	2	0	0	465	0	0	-	0	0	0	0	326	0	49	0
100- 75	-	-	-	0	710	4	148	-	0	0	2	45	0	0	0	0	0	0	15	0	0	0	97	0	5	0
225-100	0	-	0	0	5	-	760	1195	-	0	535	45	0	0	0	0	0	0	0	0	0	0	130	0	137	0
350-225	0	-	0	0	0	0	0	0	-	-	0	0	-	-	-	0	0	-	0	0	0	0	0	0	0	0
475-350	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
600-475	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
																							937	0	450	0
															Polygastric average D/N total: 1387/2 =							693				
															Eudoxid average D/N total:							0				
6911-12																										
25- 0	0	0	248	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27	0	0	0
50- 25	0	0	15	-	-	-	-	-	0	-	0	0	0	-	0	0	-	0	0	0	0	0	1	0	0	0
75- 50	0	0	92	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	11	0	0	0
100- 75	0	-	87	-	-	-	-	-	0	0	0	-	-	-	-	0	-	0	0	0	0	0	14	0	0	0
225-100	-	0	0	-	-	-	-	-	-	-	0	-	0	0	0	0	-	0	0	-	0	0	0	0	0	0
350-225	0	0	0	-	-	-	-	-	-	-	0	0	-	-	0	0	0	0	0	0	-	0	0	0	0	0
475-350	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	0	0	0	0	-	0	0	0	0	0	0
600-475	0	0	0	-	-	-	-	-	-	-	-	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0
																							53	0	0	0
															Polygastric average D/N total: 53/2 =							26				
															Eudoxid average D/N total:							0				

* Eudoxid

Table 2. Seasonal day/night bathymetric distribution of *Chelophyes appendiculata* (polygastric and eudoxid* stages) during 1969.

Sta.	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		120.90		Total Average			
Depth	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	Day		Night	
																							Poly.	Eudox.	Poly.	Eudox.
6902-03																										
25- 0	32	154 + 34*	89	3	-	-	-	-	8	2	49 + 208*	21	-	-	0	2	51 + 58*	115 + 48*	46	90	14	83	36	33	58	10
50- 25	-	207	104	6	-	-	-	-	120*	18	38 + 35*	62	-	-	0	0	-	54	14	36	8*	7	26	27	48	0
75- 50	16	-	89 + 74*	-	-	-	-	-	5 + 5*	92*	43	30	-	-	0	0	-	3	28	8	-	-	30	13	8	18
100- 75	10	-	0	-	-	-	-	-	0	1 + 183*	24 + 35*	8	-	-	0	0	0	42	7	7	16	29	7	4	16	13
225-100	-	-	80	-	-	-	-	-	25	-	123	-	-	-	116	-	-	0	-	0	85 + 21*	134	85	4	44	0
350-225	-	-	35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	17	0	-	-
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
																							201	81	174	41
Polygastric average D/N total: 187 Eudoxid average D/N total: 61																										
6905-06																										
25- 0	1	26	120	81	40	5	8 + 2326*	83 + 416*	-	20	42	97	40 + 1000*	30 + 706*	19	80	76 + 9*	45	218 + 102*	59	3	1	37	1243	47	12
50- 25	0	5	8	40	52	225	-	0	-	2	116	141	293 + 3244*	85	4	20	1	23	2	14	-	0	59	405	55	0
75- 50	1	0	8 + 16*	2	1 + 1*	2	-	2	-	2	101	26	1540	2	4	2	1	10	0	1	0	0	184	2	4	0
100- 75	11	0	11	1	2	0	-	24 + 30*	-	5	12	5	-	70 + 302*	14	18	-	180	-	12	-	0	5	0	25	30
225-100	0	115	0	0	100	40	50	5	-	45	50	10	-	30	10	0	10	70	10	0	-	0	32	0	27	0
350-225	-	0	0	0	60	5	15	0	-	25	84	75	-	-	5	0	0	0	30	-	-	0	27	0	11	0
475-350	0	0	0	0	0	0	5.	0	-	0	15	5	-	115	60	0	0	0	0	0	0	0	9	0	10	0
600-475	0	0	0	0	0	0	-	0	-	0	0	0	-	5	0	15	0	-	0	0	-	0	0	0	2	0
																							353	1650	181	42
Polygastric average D/N total: 534/2 = 267 Eudoxid average D/N total: 1690/2 845																										
6908-09																										
25- 0	-	-	-	6	-	2	-	85	0	1	16	102	385	110	0	5	19 + 81*	8	1	256	62	36	69	11	61	0
50- 25	-	-	-	4	16	2	3	475	0	1	10	61	186	411 + 1*	0	4	-	13	24	370	0	4	29	[illegible]	135	0.1
75- 50	-	-	-	0	61	2	195	0	0	0	-	2	9	74	0	2	61	-	1	9	2	0	41	0	9	0
100- 75	-	-	-	0	6	0	12	-	2	2	11	0	0	52	0	0	2	30	1	6	0	0	4	0	10	0
225-100	15	-	40	0	15	-	565	60	-	5	50	10	285	420	330	0	130	15	40	30	20	10	149	0	61	0
350-225	15	-	10	40	0	0	355	5	-	-	45	0	-	-	-	0	10	-	380	20	15 + 5*	30	13	0.6	15	0
475-350	0	-	0	0	0	0	0	0	0	0	0	0	0	30	0	75 + 75*	0	0	0	15	0	0	0	0	12	7
600-475	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	165	0	0	0	0	0	0	0	0	23	0
																							305	11.6	326	7.1
Polygastric average D/N total: 628/2 = 314 Eudoxid average D/N total: 18/2 = 9																										
6911-12																										
25- 0	4	13	15	-	-	-	-	-	3	140	32	84	76	3	0	0	90*	50	0	0	38	95	17	10	48	0
50- 25	1	0	0	-	-	-	-	-	3	-	62	174	5	-	0	0	-	91	0	2	53	75	15	0	56	0
75- 50	20	0	2	-	-	-	-	-	-	-	56 + 1*	288	6	-	0	3	4	-	0	1	0	11	11	0.1	60	0
100- 75	2	-	56	-	-	-	-	-	0	18	4	-	-	-	-	1	-	0	4	0	1	3	11	0	4	0
225-100	-	0	30	-	-	-	-	-	-	-	260	-	460	75	30	30	-	5	20	-	20	20	131	0	26	0
350-225	0	0	0	-	-	-	-	-	-	-	145	120	-	-	0	35	0	0	20	0	-	0	27	0	25	0
475-350	0	0	0	-	-	-	-	-	-	-	80	0	10	-	0	0	0	0	0	-	0	0	11	0	0	0
600-475	0	0	0	-	-	-	-	-	-	-	-	10	0	-	-	0	0	0	0	0	0	0	0	0	1	0
																							223	10.1	220	0
Polygastric average D/N total: 443/2 = 221 Eudoxid average D/N total: 10/2 = 5																										

Table 3. Seasonal day/night bathymetric distribution of *Eudoxoides spiralis* (polygastric and eudoxid stages) during 1969.

Sta.	70.60		70.75		70.90		70.110		90.45		90.60		90.90		120.45		120.55		120.70		* 120.90			Total Average Day		Total Average Night	
Depth	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N		Poly.	Eudox.	Poly.	Eudox.
6902-03																											
25- 0	0	0	0	17*	-	-	-	-	0	0	0	0	-	-	0	9	117 19*	170 359*	335 265*	596 323*	28 20*	278 133*		60	38	168	108
50- 25	-	0	0	0	-	-	-	-	0	0	0	0	-	-	0	0	-	197 84*	518 232*	530 156*	42 21*	78 50*		260	42	101	40
75- 50	0	-	0	-	-	-	-	-	0	0	0	0	-	-	0	0	-	78 69*	392 1464*	390 40*	-	-		65	24	93	21
100- 75	0	-	0	-	-	-	-	-	0	0	0	0	-	-	0	0	0	65 48*	45 24*	43 50*	10	54 35*		9	2	27	22
225-100	-	-	0	-	-	-	-	-	0	-	0	-	-	-	0	-	-	0	-	33*	133 165*	0		33	41	0	0
350-225	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-		0	0	-	-
475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
																								426	147	385	191
															Polygastric average D/N total: 815/2 =							407					
															Eudoxid average D/N total: 348/2 =							174					
6905-06																											
25- 0	0	0	0	0	0	0	0	184 385*	-	0	0	2	0	16 184*	0	1	0	0	0	33 24*	30* 154*	16*		3	13	21	55
50- 75	0	0	0	0	0	0	-	408 418*	-	0	0	0	9266*	30 45*	0	0	1	58*	3 5*	16*	-	33 8*		0.5	1158	42	49
75 -50	0	0	0	0	0	0	-	180	-	0	0	0	216 1078*	106*	0	0	0	0	0	0	1	0		24	118	16	9
100- 75	0	0	0	0	0	0	-	6	-	0	0	0	-	0	0	2	-	0	-	5 8*	-	0		0	0	1	0
225-100	0	0	0	0	0	0	0	5	-	0	0	0	-	0	0	0	0	0	0	0	-	0		0	0	0.4	0
350-225	-	0	0	0	0	0	0	5	-	0	0	0	-	-	0	0	0	0	0	-	-	0		0	0	0.5	0
475-350	0	0	0	0	0	0	0	5	-	0	0	0	-	0	0	0	0	0	0	0	0	0		0	0	0.4	0
600-475	0	0	0	0	0	0	-	0	-	0	0	0	-	0	0	0	0	-	0	0	-	0		0	0	0	0
																								27	1289	81.3	113
															Polygastric average D/N total: 108/2 =							54					
															Eudoxid average D/N total: 1402/2 =							701					
6908-09																											
25- 0	-	-	-	0	-	0	-	2	0	0	30 60	0	423 375*	45 15*	0	0	15 16*	0	45*	105				78	82	16	1
50- 25	-	-	-	0	0	0	0	0	0	0	31	1	165 168*	360 325*	0	0	-	0	132 16*	91				46	26	50	36
75- 50	-	-	-	0	15	0	0	0	0	0	-	0	0	45	0	0	14 14*	-	1	0				4	2	9	0
100- 75	-	-	-	0	0	0	0	-	0	0	0	1	0	0	0	0	0	15	0	0				0	0	2	0
225-100	0	-	0	0	0	-	0	5 300*	-	0	0	0	0	0	0	0	0	0	0	70				0	0	9	37
350-225	0	-	0	0	0	0	0	5	-	-	0	0	-	-	-	0	0	-	0	0				0	0	0	0
475-350	0	-	0	0	0	5	0	0	0	0	0	0	5	10	0	0	0	0	0	0				0	0	1	0
600-475	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0	0
																								128	116	87	74
															Polygastric average D/N total: 215/2 =							107					
															Eudoxid average D/N total: 184/2 =							92					
6911-12																											
25- 0	0	0	15	-	-	-	-	-	0	0	30*	0	236 360*	90 30*	0	0	0	0	0	0	15	45 60		29	43	16	11
50- 75	0	0	0	-	-	-	-	-	0	-	0	76	81 90*	-	0	0	-	0	0	0	16	0		12	11	12	0
75- 50	2	0	0	-	-	-	-	-	-	-	1	0	31	-	0	0	0	-	0	0	0	0		4	0	0	0
100- 75	0	-	0	-	-	-	-	-	0	0	2	-	-	-	-	0	-	0	0	0	0	0		0	0	0	0
225-100	-	0	0	-	-	-	-	-	-	-	0	-	530 675*	0	0	0	-	0	0	-	0	0		88	112	0	0
350-225	0	0	0	-	-	-	-	-	-	-	0	0	-	-	0	0	0	0	0	0	-	0		0	0	0	0
475-350	0	0	0	-	-	-	-	-	-	-	0	0	0	-	0	0	0	0	0	-	0	0		0	0	0	0
600-475	0	0	0	-	-	-	-	-	-	-	-	0	-	-	0	0	0	0	0	0	0	0		0	0	0	0
																								133	166	28	11
															Polygastric average D/N total: 161/2 =							80					
															Eudoxid average D/N total: 177/2 =							88					

* Eudoxid stage

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DIFFERENCES IN HEART SIZE BETWEEN OCEAN-CAUGHT AND LABORATORY-GROWN LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* Girard

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Abstract: Large differences in heart size occur between ocean-caught and laboratory-grown larvae of the northern anchovy, *Engraulis mordax* Girard. At 4 mm in standard length (3 days), laboratory-grown larvae had hearts only slightly larger than ocean-caught larvae, but at 9 mm (16 days), hearts of laboratory-grown larvae were 40% longer. Thereafter, the percentage decreased to 24% at 19 mm, the longest laboratory-grown larvae available. The percentage probably decreases further in larvae longer than 19 mm as indicated by trends in the allometric growth equations. At the first-feeding stage in the laboratory, larvae that had been feeding for 2 days had larger hearts and deeper bodies than non-feeding larvae.

INTRODUCTION

While examining ocean-caught and laboratory-grown anchovy (*Engraulis mordax* Girard) larvae, side-by-side, it became apparent that there was a substantial difference in heart size between larvae of these two types. As heart size might be associated with other morphological and apparent behavioral differences (Arthur, 1976), an examination of heart size of ocean-caught and laboratory-grown larvae over the length ranges available was conducted.

METHODS AND MATERIALS

All larvae examined had been preserved in 4% formalin. Laboratory-grown larvae were from three groups reared at the Southwest Fisheries Center, La Jolla. Group 1, preservation time 1 month to 2 yr, were reared at 17 and 19 °C on a diet of laboratory-reared dinoflagellates, rotifers, and copepods (Hunter, 1976). Group 2, preservation time 8 yr, were reared on wild plankton at 17 °C in 1968 (Kramer & Zweifel, 1970). Group 3, preservation time 9 yr, were reared on wild plankton at an unknown temperature. Ocean-caught larvae came from January, April and July California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises from 1963 and 1965. There should be no effect of shrinkage on body length between the groups, as Blaxter (1971) found no consistent shrinkage in herring larvae after the first day of preservation.

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Measurements were made with an ocular micrometer of specimens immersed in glycerine. All body length measurements of larvae were standard length. The ventricle was used as an index of heart size because it has definite anterior and posterior edges, whereas the conus tapers gradually and has no readily visible anterior boundary. Ventricle length can be measured without excising the heart but the pectoral fin must often be manipulated in order to view all edges.

RESULTS

HEART SIZE

Heart size at first feeding appears to be the same for ocean-caught and laboratory-grown larvae (Fig. 1). When larvae grew to 4.6 mm in the laboratory, most appeared to have substantially larger hearts than ocean-caught larvae, and by 5.0 mm there was little overlap between laboratory-grown and ocean-caught larvae. Hearts of 5.2 mm laboratory-grown larvae nearly fill the pericardial cavity, whereas hearts of ocean-caught larvae of the same length take up a noticeably smaller amount of space

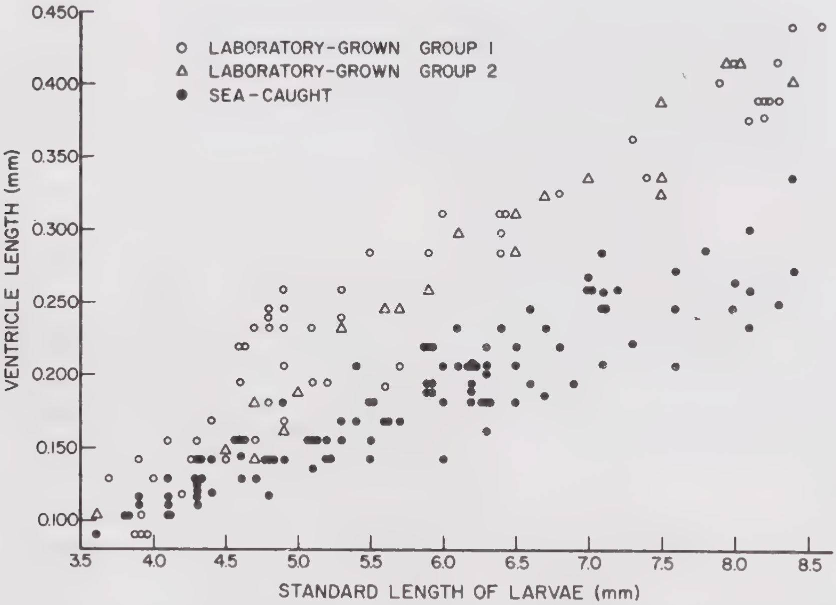

Fig. 1. Comparison of heart length near first feeding stages of ocean-caught and laboratory-grown northern anchovy larvae: see p. 99 for a description of the groups used.

(Fig. 2). Pericardial cavities seem to be about the same size for the two types of larvae. The curves for body length to ventricle length relationships in Fig. 3 were derived by using Marquardt's algorithm (Conway *et al.*, 1970) for fitting Zweifel's allometric growth model (Zweifel, unpubl.).

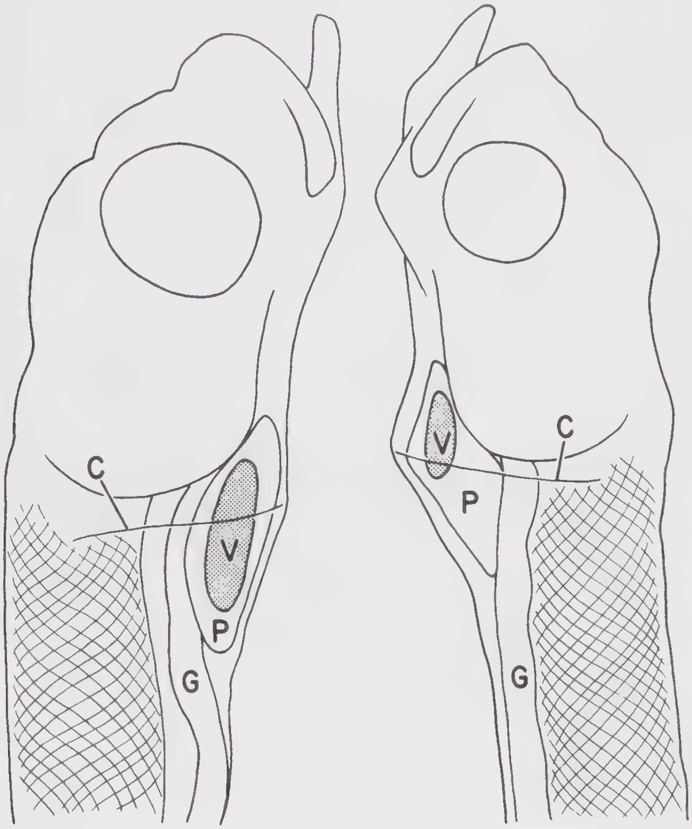

Fig. 2. Pericardial area of a typical 5.2 mm SL laboratory-grown northern anchovy larva (left) and a typical 5.2 mm SL ocean-caught anchovy larva (right): C, cleithrum; G, gut; P, pericardial cavity; V, ventricle.

$$\ln \mathrm{HL} = a - b(\mathrm{c} - \ln \mathrm{SL})^{d}.$$

HL and SL are heart length and standard length, respectively. Zweifel noted that the parameter b has no simple biological meaning, a corresponds to the logarithm of the maximum heart length, c represents the logarithm of the maximum standard length, and d is the ratio of the rates of change with time of the separate instantaneous growth rates (Laird, 1965). When $d = 1$, this equation becomes $\ln \mathrm{HL} = a + b \ln \mathrm{SL}$, the equation of simple allometry. Zweifel conducted an analysis

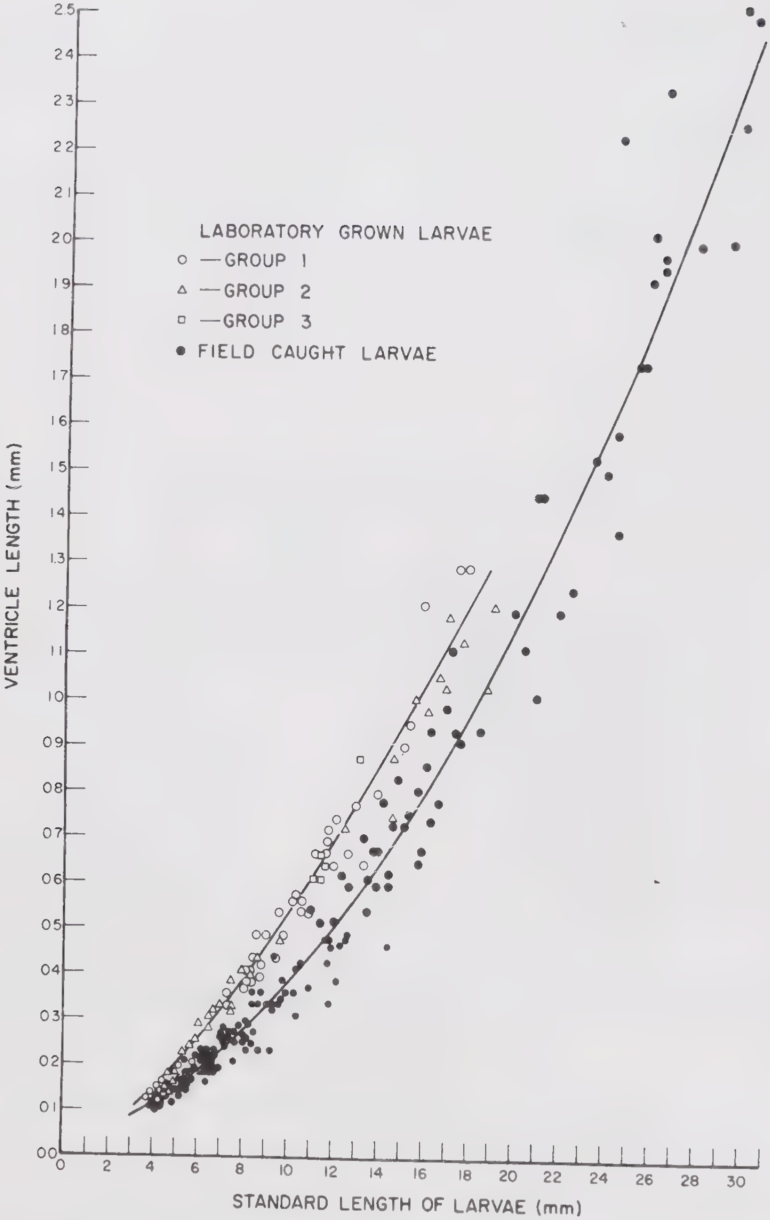

Fig. 3. Heart length to body length relationships of laboratory-grown and ocean-caught northern anchovy larvae: the line for laboratory-grown larvae was calculated from $\ln HL = 1.2994 - 0.2742(5.0563 - \ln SL)^{1.9122}$; the line for ocean-caught larvae was calculated from $\ln HL = 2.4309 - 2.5230(3.8764 - \ln SL)^{0.6549}$; see p. 99 for a description of the groups used.

of covariance of these data and found no difference in the slopes of the curves in Fig. 3 but a highly significant difference in their elevations.

The greatest percentage difference between body length and ventricle length occurred at 9 mm where hearts of laboratory-grown larvae averaged 40% longer. Thereafter, the percentage decreased to 24% at 19 mm, the longest laboratory-grown larvae available. Extrapolating from equations in Fig. 3 heart length differences became negligible at about 32 mm although Zweifel warns that extrapolating outside the range of observations must be done with caution.

EFFECTS OF FEEDING AND STARVATION ON HEART SIZE

The usual numbers of copepod nauplii in the ocean have seldom been found (Arthur, 1977) to equal those required for the laboratory rearing of anchovy larvae (Kramer & Zweifel, 1970; O'Connell & Raymond, 1970) although *Gymnodinium splendens* occurs in the ocean at times in high enough concentrations to support life over a short larval period (Lasker, 1975). It therefore seems reasonable to suppose that the small size of hearts of ocean-caught larvae might be associated with poor feeding conditions. To test this supposition, a group of first feeding anchovy larvae were placed in a container with *G. splendens* (100/ml) while another group from

TABLE I

Comparison of ventricle lengths and body depths of starved and fed (after two days of feeding) anchovy larvae from the same egg source.

	Fed	Starved	Fed / starved	*t* (independent)
Number of larvae	29	33		
Mean ventricle length (mm) ± SD	0.1250 ± 0.0269	0.0919 ± 0.0124	1.360	6.3457, *P* = <0.001
Mean body depth (mm) ± SD	0.4350 ± 0.0311	0.4036 ± 0.0208	1.078	4.6617, *P* = <0.001

TABLE II

Comparison of ventricle lengths and body depths of feeding and non-feeding anchovy larvae living in the same aquarium after two days exposure to food.

	Feeding	Non-feeding	Feeding / non-feeding	*t* (independent)
Number of larvae	20	9		
Mean ventricle length (mm) ± SD	0.1358 ± 0.0225	0.0989 ± 0.0158	1.373	4.4109, *P* = <0.001
Mean body depth (mm) ± SD	0.4509 ± 0.0257	0.3999 ± 0.0298	1.128	5.1407, *P* = <0.001

the same laboratory-spawned egg source (Leong, 1971) were placed in a container with filtered sea water. After 2 days, both groups of larvae were preserved in 4% formalin. Ventricle length as well as body depth were significantly larger in the fed group (Table I). The fed group was introduced to food 1 day after yolk absorption, which is near the point of "irreversible starvation" (1.5 days after yolk absorption, Lasker *et al.*, 1970) when most northern anchovy larvae refuse to feed even when presented food. Apparently as a result of this delayed exposure to food nine of the 29 larvae had not eaten, as was indicated by their unexpanded guts. Differences in ventricle length and body depth between feeding and non-feeding individuals of these 29 larvae was significant (Table II).

DISCUSSION

There is evidence of several apparent morphological and behavioral differences between ocean-caught and laboratory-grown anchovy larvae (Arthur, 1976). Ocean-caught larvae, as opposed to laboratory-grown larvae: (1) do not increase the size of food particles ingested in proportion to increasing length for larvae larger than 4 mm; (2) show a steep decline in feeding incidence (percentage of larvae containing food) beginning at the 4.5 mm length to about 7.0 mm; and (3) undergo a decline in relative morphological condition (as measured by body depth) until they have attained a length of 17 to 18 mm. It was suggested that the lack of increase in food particle size and the decrease in feeding incidence indicated that most anchovy larvae in the ocean decreased their feeding activity after first feeding and fed on food items only in their immediate environment (which are mostly of the smaller sizes ingested at first feeding, Arthur, 1977). This suggestion is supported by the small hearts of ocean-caught anchovy larvae, because heart size probably indicates the activity level of swimming and feeding. Changes in cardiac output in fish are normally associated with large changes in stroke volume and small changes in heart rate, whereas increased cardiac output in mammals is usually associated with large changes in heart rate but with little change in stroke volume (Randall, 1968). The abundance of food in the laboratory may stimulate increased predatory activity, and therefore heart size, over that occurring in the ocean. Production of noradrenaline and adrenaline associated with cardiac output in teleosts (Randall, 1968) is markedly increased in trout larvae at the onset of first feeding (Meyer & Sauerbier, 1977). Heart-volume to body-volume ratios for active surface marine teleosts such as barracuda, 0.24%; mackerel, 0.20%; and salmon, 0.19–0.36% are higher than those of demersal fishes such as cod, 0.15% and haddock, 0.17% (Spector, 1956). Kishinouye (1923) noted that the tunas, which are characterized by swift and unceasing locomotion, have notably larger hearts than other scombroid fishes.

The large hearts of laboratory-grown larvae might partly be a result of laboratory conditions. Blaxter (1975) noted various morphological, behavioral and physiological differences between reared and wild fish. Activity and therefore heart size of larvae in the laboratory may be unnaturally high because of noises, or contact with walls or bottoms of aquaria, or contact with each other. This argument, however, does not explain the increase in heart size of older ocean-caught larvae in relation to that of laboratory-grown larvae. The large hearts of laboratory-grown larvae may also be partly a result of low oxygen availability, as oxygen content of rearing tanks is often less than that of the open ocean (Hunter, pers. comm.). Hunter (1972) reported that anchovy larvae spend more time swimming when in water with oxygen concentrations below saturation than in saturated water. Heart size, however, is more closely associated with feeding as indicated by the larger hearts of feeding than non-feeding larvae in the same container (Table II) and therefore at the same oxygen saturation.

Fish larvae with limited energy stores, such as first-feeding sardines and anchovies, cannot afford to waste much energy on unrewarded feeding activities. By the time a sardine larva has consumed all of its yolk and is ready to feed it is already in a metabolic deficit (Lasker, 1962). Emaciation as a result of unsuccessful feeding activities might be seen in the results of O'Connell (1976). He observed that most of the 2-day-old anchovy larvae reared with food (*Gymnodinium*) present were in poorer physical condition than larvae of the same age that had not been exposed to food. O'Connell suggested that the larvae with no food available were not stimulated to expend energy for feeding activities whereas most larvae exposed to food had been stimulated to capture food but had not been successful because of the brief learning period and/or low food density.

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At high speeds dolphins save energy by leaping

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An observer may wonder whether a school of 'running' dolphins, consisting of numerous, wildly splashing individuals, is using the most efficient mode of locomotion, because splashing wastes energy. Dolphins exhibit at least three modes of swimming. In leisurely, unhurried motion, they break the surface briefly and gently, often showing little more than the blowhole. At a faster, 'cruising' speed, frequently at 3–3.5 ms^{-1} (6–7 knots), the animals are seen swimming primarily just beneath the surface, and there is still little splashing. (Behaviour and speeds of dolphin schools were observed from a helicopter and will be described elsewhere by D. A. and W. Perryman.) Swimming speeds in this mode have been measured up to 4.6 ms^{-1} (9.3 knots). But in the fastest 'running' mode, the animals clear the water in sequential, parabolic leaps, accompanied by considerable splashing on exit and re-entry (Fig. 1). Leaps are interspersed with relatively brief, subsurface swimming. This swimming is common when dolphins are alarmed by vessels approaching within 500 m. We have examined dolphin swimming in terms of energy required per unit distance travelled and report here that beyond a certain 'crossover' speed, leaping must be more efficient than swimming.

The energy cost of leaping must be compared with that of continuous swimming very close to the surface. This is because during rapid swimming, as in escape behaviour, the rate of respiration increases, and the animals are therefore constrained to the surface layer. The extra energy required for jumping is approximately (neglecting air resistance)

$$J = WH\,(1+m) \tag{1}$$

where W is the weight of the dolphin, H is the maximum height of the centre of gravity above the undisturbed sea level, and m is a correction term accounting for the spray carried along with the dolphin as it emerges. The dolphin is approximately neutrally buoyant[1] and so very little energy is required to raise the centre of gravity to surface level. The energy in equation (1) will be compared with that expended by a dolphin swimming continuously with its blowhole just out of the water. This swimming would be roughly equivalent to that of leisurely or cruising swimming, where no more than one-third of the body is out of the water at any instant.

The energy required for swimming at one equivalent body radius beneath the undisturbed surface (that is just submerged) is

$$E = DL \tag{2}$$

where D is the hydrodynamic drag and L is the distance travelled. The drag can be written as[2]

$$D = \tfrac{1}{2}\rho_\omega\, V^{2/3}\, C_D \gamma U^2 \tag{3}$$

where ρ_ω is the density of water, V is the dolphin volume, C_D the drag coefficient in deep water, γ the correction due to proximity to the surface[3,4], and U the swimming speed. Dolphins usually leap only for short periods so that other energy saving aspects of swimming, as when using beat-and-glide or diving[5], are not applicable.

We now write the ratio of energy J/E to find the range of speeds at which this ratio is <1, that is leaping is energy sparing.

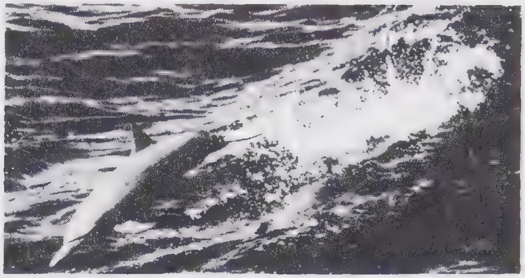

Fig. 1 A 'running' eastern spinner dolphin (*Stenella longirostris*) leaping approximately two body lengths in the rapid swimming mode. Photograph by R. Pitman.

The energies must be compared over the same distance and therefore the length of the jump as a function of swimming speed has to be known. We neglect air resistance. The leaping dolphin has an approximate ballistic trajectory, for which the distance crossed while the centre of gravity of the animal is out of the water is

$$L = \frac{U^2}{g}\sin 2\alpha \tag{4}$$

where g is the gravitational constant and α the emergence angle, measured from the horizon. The maximum height reached by the centre of mass is

$$H = \frac{U^2 \sin^2\alpha}{2g} \tag{5}$$

The longest leap for given speed U is obtained when $\alpha = 45°$. In this case, designated by subscript 'max',

$$L_{\text{max}} = \frac{U^2}{g};\ H_{\text{max}} = \frac{U^2}{4g} \tag{6}$$

Using these results, we obtain the ratio J/E:

$$R = \frac{J}{E} = \frac{\rho_d g V \dfrac{U^2}{4g}(1+m)}{\frac{1}{2}\rho_\omega V^{2/3} C_D \gamma U^2 \dfrac{U^2}{g}} = \frac{\rho_d g (1+m) V^{1/3}}{2\rho_\omega C_D \gamma U^2} \tag{7}$$

where ρ_d is the density of the dolphin. Equation (7) shows that for a given dolphin swimming as described, the ratio R decreases monotonically as forward speed U increases. Thus, for every species, there will be a range of speeds for which leaping will be more efficient than shallow swimming. The lowest (crossover) speed at which this occurs is obtained by setting $R = 1$ in equation (7). This speed U_c is dependent on the size of the dolphin (through the volume V), its density, its shape (which will define C_D and m), and how far beneath the surface it swims (which defines γ).

To obtain specific values of the crossover speed, we substitute typical values of the different parameters in equation (7). The dolphin's density is affected by the degree of lung inflation and the extent of fat reserves. We take it to be approximately equal to the density of sea water[1], that is, $\frac{\rho_d}{\rho_\omega} = 1$. The spray mass coefficient is obtained from the longitudinal added mass, defined as the mass of water carried along when a body moves through a fluid. Thus when the dolphin leaves the water, this mass is carried along. The added mass coefficient for fusiform, elongated shapes such as the dolphin's is[6] $m \simeq 0.2$. Hoerner[2] gives the relationship between the drag coefficient C_D based on volume and skin frictional drag C_f as

$$C_D/C_f = 4(l/d)^{1/3} + 6(d/l)^{1.2} + 24(d/l)^{2.7}$$

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which gives a ratio of 8 for a dolphin with an l/d ratio of about 5, where d = diameter and l = length. Hoerner's Fig. 22 shows C_f to be between 0.002 and 0.003 for semi-turbulent flow in the appropriate range of Reynolds number, so that C_D was approximated here as 0.02. The surface effect correction γ is taken as 4.5 when the body is fully submerged, just below the surface. (If the dolphin were an exact body of revolution $\gamma = 5$)[3,4]. Both C_D and γ should be considered approximations, C_D because it may be a conservative estimate for a flexing body and γ because it is sensitive to submerged depth and decreases rapidly to 1 at a depth three times the body diameter. Substituting all the above values in equation (7) and setting $R = 1$, we obtain

$$U_c = 65.3\,V^{1/3}$$

where U_c is in $\mathrm{m\ s^{-1}}$ and V in $\mathrm{m^3}$. This general equation, while only an approximation for any specific dolphin, should give a good estimate of the expected speeds above which leaping will occur. Table 1 gives the values of the crossover speed, U_c, as a function of body volume.

Table 1 Predicted values of crossover speed U_c over which leaping becomes energy sparing as a function of body volume

V ($\mathrm{m^3}$)	U_c ($\mathrm{m\ s^{-1}}$)	L_C (m)	H_C (m)	E (J)
0.005	3.34	1.14	0.28	17
0.05	4.90	2.45	0.61	368
0.1	5.50	3.09	0.77	928
0.15	5.89	3.54	0.88	1,590
0.2	6.18	3.90	0.97	2,340
0.25	6.41	4.19	1.05	3,160
1	8.08	6.66	1.67	20,100
5	10.57	11.40	2.85	172,000

Predicted leap length and height are shown, as well as the energy required for each leap ($g = 9.8\ \mathrm{m\ s^{-2}}$). For any given volume, underwater motion at less than U_c is less energy-consuming than leaping the same distance. A volume of 1 $\mathrm{m^3}$ corresponds to a weight of 1,025 kg.

Table 1 indicates that for the usual size range (0.05–0.10 $\mathrm{m^3}$) of most dolphin species[7,8], the crossover speed is about 5 $\mathrm{m\ s^{-1}}$ (10 knots), well within their available range of speeds[9]. During January and February 1977 and 1979, the RV David Starr Jordan approached various dolphin species (*Stenella* spp., *Delphinus delphis*) at speeds of 4.5–5 $\mathrm{m\ s^{-1}}$ (9–10 knots) in the eastern tropical Pacific. At that speed, the vessel could approach close to all schools as long as they could be tracked. However, it often took an hour for the ship to close onto schools initially seen at about 2 miles (3.6 km) distance. Evidently those dolphins were mostly moving at cruising speeds of 3.5–4 $\mathrm{m\ s^{-1}}$ (7–8 knots), similar to previous measurements. We observed that the leaping (running) mode occurred primarily after the ship had closed to within 500 m and the animals had become increasingly alarmed and had noticeably increased speed. No measurements of actual speed were possible as the leaping dolphins usually escaped abeam and when followed, continued along curved paths. The speeds attained appeared somewhat greater than that of the ship and were probably in excess of the crossover speed. The actual crossover speed is probably within 10% of the predicted value. Thus, because of their shallow swimming ($\gamma = 4.5$), the crossover speed must be approximately 5 $\mathrm{m\ s^{-1}}$ (10 knots), and dolphins must leap to obtain higher speeds efficiently.

Swimming speed can be estimated indirectly by measuring the distance between the emergence spot and the re-entry splash on photographs similar to Fig. 1, and comparing it to animal length. These distances were within the range of 2–4 m, as expected from Table 1. The height of the leaps (to the centre of gravity) is between 0.6 and 1.0 m, also in agreement with Table 1. Spotted and spinner dolphins (*S. attenuata* and *S. longirostris*) have been observed leaping distances of about three body lengths (5.4 m) when chased closely by speedboats, corresponding to a swimming speed of ~7.3 $\mathrm{m\ s^{-1}}$ (14.6 knots)[10]. After escaping purse seine nets, they continued leaping for 1,500 m, performing leaps of ~2.3 body lengths, which corresponds to a speed of 6.4 $\mathrm{m\ s^{-1}}$, also greater than the crossover speed.

Larger cetaceans ($V > 1\ \mathrm{m^3}$, weight > 1 ton) probably cannot leap during fast swimming, as the energy required for leaping increases rapidly with body size (Table 1). Fishes, on the other hand, do not have to break surface to breathe and can stay sufficiently deep for surface proximity effects to be negligible ($\gamma = 1$). Crossover speed would then be increased by a factor of more than 2, and, except for large fish such as istiophorids and some large scombrids, is not likely to be an important factor in swimming.

Although the cetacean running mode has been described in the context of escape behaviour, it could occur in any situation where rapid speeds for short periods were required. Furthermore, leaping behaviour is not restricted to the running mode. At any speed, individual dolphins will often 'splash leap', that is leap out of the water with various contortions so as to re-enter with a large splash. The various attitudes of such leaps indicate, however, that they are not primarily related to horizontal velocity. Their function is most probably that of display–communication, the exact meaning depending on the situation, including the physiological state of the animal.

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Atmospheric Response to SST Anomalies

For the past year a spectral General Circulation Model of the Climate Dynamics Group of NOAA's Geophysical Fluid Dynamics Laboratory (GFDL) (Manabe, *et al.*, 1978) has been used in numerical experiments to improve our understanding of the physical mechanisms operating in the Walker Circulation and the Southern Oscillation.

The model is global and has spectral truncation at 15 waves using the "rhomboidal" truncation. It has 9 σ levels in the vertical. Nonlinear terms are calculated in the grid domain after transformation of the variables from the spectral domain. For the computation of radiation the seasonally varying isolation is prescribed at the top of the atmosphere, and a zonally uniform cloud cover is assumed.

Equatorial Anomalies

The model has a hydrologic cycle. Surface temperature over land is determined by the routes discussed in the earlier article were covered.

Temperature maps at standard depths are produced using objective analysis techniques (Gandin, 1963) to interpolate the data to a the condition of no heat storage in the soil. Seasonally varying sea surface temperatures are prescribed. For these experiments warm sea surface temperature anomalies over different parts of the equatorial Pacific were used (Figure 1). The anomaly was introduced in the middle of March; integrations were carried out until the end of August, and the anomalous response was studied June-August. The statistical significance of the response was assessed.

Walker Circulation

Precipitation increased near the anomalies and decreased slightly to the west. The induced heat sources (precipitation anomalies) produced global-scale anomalies in the equatorial zonal winds, especially in the upper troposphere and in the sea level pressure. Figure 2(a,b,c) shows the east-west anomaly circulations induced in the equatorial atmosphere by the sea surface temperature anomalies over the eas[illegible] mapping procedure for the equatorial Pacific is a prototype. The statistical structure used for objective analysis reflects the fact that energetic interannual fluctuations in sea level and baroclinic structure have a spatial scale on the order of 1000 km (Wyrtki, 1979). The grid in this area was 2°-latitude by 10°-longitude. A network analysis to improve the mapping procedure is being developed. Specification of the necessary autocorrelation functions and signal-to-noise ratios will be made as accurately as historical data permits. the equatorial Pacific a Walker Circulation occurs with easterlies in the lower levels and westerlies in the upper levels, with ascent over the vicinity of Indonesia and descent over the eastern Pacific. Thus, warm anomalies over the eastern Pacific tend to weaken the Walker Circulation and similar ones over the western Pacific tend to strengthen it. These circulation anomalies were found to be statistically significant. Besides these equatorial and tropical anomalies a significant strengthening of the subtropical westerlies occurs principally in the winter hemisphere in the general longitude of the anomalies.

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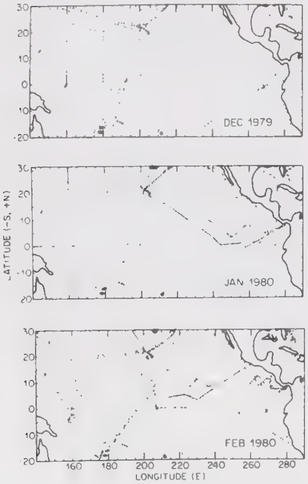

FIGURE 1 *(Meyers & Guberek)*

XBT observations in the tropical Pacific from top to bottom, December 1979, January 1980 and February 1980; observations from the Hawaii-Tahiti Shuttle Experiment were not plotted.

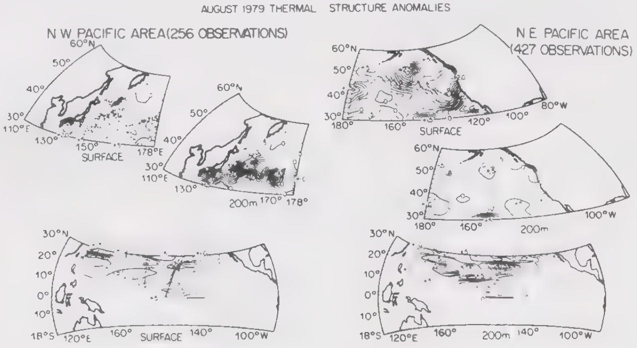
AUGUST 1979 THERMAL STRUCTURE ANOMALIES
N W PACIFIC AREA(256 OBSERVATIONS)
N E PACIFIC AREA (427 OBSERVATIONS)
SURFACE
200m
60°N
50°
40°
30°
110°E
130°
150°
170°
178°E
180°
160°
120°
100°
80°W
100°W
30°N
20°
10°
0°
10°
18°S
120°E
140°
EQUATORIAL PACIFIC (360 OBSERVATIONS)

FIGURE 2 *(Meyers & Guberek)*

Objective analysis of temperature anomalies in August 1979

Cetaceans and Equatorial Oceanography

More evidence of the distinctiveness of the equatorial cetacean community was obtained during the 21 March-19 April 1980 trans-Pacific voyage of the NOAA ship *Oceanographer*. Two biologists from the Southwest Fisheries Center (SWFC) in La Jolla were aboard during the San Diego-Kwajalein EPOCS voyage that transited the equator between 110°W and 175°E longitude. Using 25 × 150 mm binoculars, they searched both for seabirds and cetaceans along the cruise track and logged 162 separate sightings of cetacean schools. Their sighting rate, up to 34 sightings/100 track miles searched, indicates that equatorial waters at times support a major cetacean community. The *Oceanographer* voyage provided a rare opportunity to collect detailed data on the distribution of cetaceans in the poorly known eastern and central equatorial Pacific.

The concentration of cetaceans is related to oceanographic conditions.

Large baleen whales and pilot whales were the animals most frequently sighted, followed by the beaked whales. Among the latter, Cuvier's beaked whale (*Ziphius cavirostris*), a species not generally considered equatorial, was abundant between 110°W and 115°W. Very few spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*), the characteristic species of eastern tropical Pacific waters, were seen. They were replaced along the equator by another species pair that also forms large schools, Fraser's dolphin (*Lagenodelphis hosei*) and the melon-headed "whale" (*Peponocephala electra*). Both of these dolphins have been described only recently in the eastern Pacific (Perrin *et al.*, 1973; Perrin, 1976), where continuing studies have suggested that they are primarily equatorial in distribution. This now appears confirmed as 13 (possibly 21) schools of Fraser's dolphins and/or melon-headed whales were seen from the *Oceanographer*, more than on any other research cruise. Another interesting species, also abundant between 110°W and 115°W, was the "rare" dwarf sperm whale (*Kogia simus*) which was sighted 10 times during the cruise.

The concentration of cetaceans along the equator appears related to distinct oceanographic conditions there (Figure 1). A conspicuous feature is the relatively weak thermocline gradient and often the absence of a mixed layer. East of 145°W surface divergence and the effects of the undercurrent had virtually

continued page 10

Cetacean Populations and Equatorial Oceanography

from page 6

eliminated the mixed layer. Eighty-two percent of the cetaceans were seen there, and the predominant birds were the plankton-feeding storm petrels. As the surface mixed layer developed and deepened west of 145°W, these birds were rapidly replaced by great numbers (2,000-4,000/day) of sooty terns (*Sterna fuscata*), which feed commensally with surface fish. In tropical waters north of the equator, where the thermocline is strong and shallow, birds and fish are most frequently found associated with aggregations of dolphins. But along the equator the numerous sooty terns were conspicuous in their general lack of association with cetaceans. These changes in species communities relative to oceanography support the conclusions of Au, *et al.*, (1979) but have never before been so clearly demonstrated.

A major deficiency in present knowledge of eastern Pacific cetaceans is the understanding of seasonal effects. More observations from a wider band about the equator are needed, *e.g.* to study the school-aggregating effects of the seasonally intensified Equatorial Front (Au *et al.*, 1979). Further participation by SWFC cetacean biologists on EPOCS cruises are being planned.

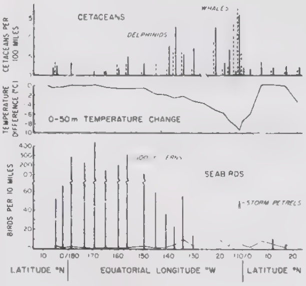

FIGURE 1(Au et al.)

Cetaceans, birds, and environment along the track of the R/V Oceanographer *21 March - 19 April 1980. The 0-50 m vertical temperature change is an index of the depth of the mixed layer.*

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University of South Alabama Ichthyological Collection (USA·C 6278). Measurements and weights are found in Table 1.

Since most records of *C. isodon* are of juveniles, there is little information on the reproductive biology of the species. Based on the cited literature and these data, pups appear to be 45-55 cm at birth. However, seasonality is uncertain as the records of Springer (1950) are not in accord with those of either Hoese and Moore (1977) or this report.

Length at maturity can be closely estimated. One male (112 cm) collected 13 July 1978 was immature—based on incomplete calcification of the claspers and incompletely developed siphon sacs, each sac being 7.5 cm long and 1.0 cm wide. The other two males (120 and 127 cm) collected 2 July 1979 and 28 June 1978 had well-calcified claspers and fully developed siphon sacs. The only literature on mature males (Springer 1950) listed lengths of 140-152 cm. Males apparently mature between 115 and 120 cm. Maturity in females must be reached at a larger size. The female collected in July 1979 was 127 cm, yet was immature with only small undeveloped ovarian eggs. The gravid female reported here was 139 cm, and those reported by Springer (1950) were 147-155 cm.

Carcharhinus isodon was only collected when similarly sized specimens of blacktip shark, *C. limbatus*, were caught: 3 *C. limbatus* (126-166 cm) with the gravid female, 12 *C. limbatus* (102-117 cm) with the 112 cm male, 2 *C. limbatus* (111 and 124 cm) with the 127 cm male, and 12 *C. limbatus* (100-130 cm) with the two specimens caught in 1979. If *C. isodon* is an uncommon straggler into the northern Gulf of Mexico it may be schooling with other sharks of like size. Sharks that school have been noted to do so by sex or size (Ford 1921).

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SHEDDING RATES OF PLASTIC AND METAL DART TAGS FROM ATLANTIC BLUEFIN TUNA, *THUNNUS THYNNUS*[1]

In 1971, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recommended that a double-tagging experiment be conducted on Atlantic bluefin tuna, *Thunnus thynnus*, to determine whether plastic or metal dart tags were more efficient and to estimate immediate and instantaneous tag shedding rates. A knowledge of shedding rates is necessary so that appropriate adjustments can be made when estimating mortality rates from tag return data. This study was begun in 1971 by the National Marine Fisheries Service (NMFS), the Woods Hole Oceanographic Institution (WHOI), and the Fisheries Research Board of Canada (FRBC). The results obtained through 1972, for 580 double-tagged bluefin tuna released during 1971 off the east coast of the United States, were reported by Lenarz et al. (1973). Their results were partially based on tags supplied by the FRBC, some of which had longer streamers than the tags supplied by WHOI. For our present analysis, we used only data from the WHOI tags.

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[1] Southeast Fisheries Center Contribution Number 80-14M.

In this paper we present the overall findings obtained through 1978 for 3,121 double-tagged bluefin tuna. These fish were released primarily from U.S. purse seine vessels fishing off the east coast of the United States from Virginia to Massachusetts from 1971 through 1977.

Methods

The U.S. double-tagging program for Atlantic bluefin tuna was conducted jointly by the NMFS and WHOI. Tags and tagging procedures were those described by the Food and Agriculture Organization (1972). All fish were tagged and released from U.S. purse seine vessels (98% of all releases) and from a few sport fishing vessels. Tagging occurred throughout the purse seine fishing season during 1971, 1973, and 1974, and at the end of the season during 1972, 1975, 1976, and 1977. The double-tagging operation was conducted entirely by John Mason during each year except 1974, when two assistants aided in the double tagging. Precise release dates were available for all of the fish. In a few instances only the month and year were known for the recapture data. In these cases, the 15th of the month was arbitrarily selected to represent the recapture date. The vast majority of returns fall into an annual cycle during which the recapture periods are approximately 2-3 summer months. The interval midpoints of the time intervals can be considered to be on a yearly cycle. Therefore, we grouped returns into "first year returns," "second year returns," etc., and calculated average days out from the individual days out for each return. Tag shedding rates were estimated using the notation and methodology of Bayliff and Mobrand (1972) for yellowfin tuna, which Lenarz et al. (1973) used for bluefin tuna and Laurs et al. (1976) used for North Pacific albacore. Chapman et al. (1965) developed the original model with the assumption of only one type of shedding which occurs at a constant instantaneous rate. Bayliff and Mobrand (1972) assumed that there are two types, Type I which occurs immediately after the fish are released and Type II, the type described by Chapman et al. (1965).

Bayliff and Mobrand's modifications[2] of the Chapman et al. (1965) approximate equations for tag returns of double-tagged fish are:

$$n_{ddk} = F\tau N_D\, \pi\rho^2 \exp-(F+X+2L)t_k \tag{1}$$

$$n_{dsk} = 2F\tau N_D\, \pi\rho(1-\rho\exp(-Lt_k)) \exp(-(F+X+L)t_k) \tag{2}$$

where n_{ddk} = number of returns of double-tagged fish retaining both tags caught during the recapture period t_k,
n_{dsk} = number of returns of double-tagged fish retaining only one tag caught during the period t_k,
F = instantaneous rate of fishing mortality,
N_D = number of double-tagged fish released,
π = proportion of tagged fish which remain alive after the Type-I mortality (immediate) has taken place,
ρ = proportion of the tags which are retained after Type-I shedding (immediate) has taken place,
X = instantaneous rate of mortality due to natural causes, Type-II tagging mortality (long term), and emigration from the fishing grounds,
L = instantaneous rate of tag shedding (Type II), and
t_k = time at the middle of the kth recapture period of length τ (k = 1, 2, 3).

From Equations (1) and (2) it follows that

$$\frac{n_{dsk}}{n_{ddk}} = \frac{2(1-\rho\exp(-Lt_k))\exp(Lt_k)}{\rho}$$

and therefore

$$\frac{n_{dsk}}{2n_{ddk}} = \frac{\exp(Lt_k)-\rho}{\rho} = \frac{\exp(Lt_k)}{\rho} - \frac{2n_{ddk}}{2n_{ddk}}.$$

Rearranging terms yields

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[2] As pointed out by Laurs et al. (1976), there was typographical error in both Bayliff and Mobrand (1972) and Lenarz et al. (1973) in Equation (2).

$$\frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = \rho\exp(-Lt_k)$$

and hence

$$\ln\frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = \ln\rho - Lt_k = Y_k$$

where Y_k is an estimate of the natural logarithm of the proportion of tags retained up to time t_k. Given n_{ddk}, n_{dsk}, and t_k, then L and ρ can be estimated using linear regression. We first estimated these parameters using the usual least-squares linear regression which assumes homoscedasticity. We also believed that it would be appropriate to consider that variability may increase as a function of time as the number of recoveries decreases. To accomplish this, a weighting factor was introduced and a weighted least-squares linear regression model was fitted to calculate values of $\ln\hat{\rho}$ and $\hat{L}$, as was done by Bayliff and Mobrand (1972). The weights for each time interval k ($k = 1, 2, 3$) were equated to the ratio of the number of returns of double-tagged fish during interval k to the total number of returns of double-tagged fish during all k-periods. This can be simply expressed as:

$$\omega_k = \frac{n_{ddk} + n_{dsk}}{\sum_{i=1}^{3} (n_{ddi} + n_{dsi})} .$$

While we consider this a reasonable first approximation of the correct weight, further investigations of the statistical properties of Y_k to formally determine the correct weighting procedure are desirable. Estimates of $\ln\rho$ and L were then made using weighted linear regression.

Results and Discussion

The double-tag releases during 1971 through 1977 and returns in 1971 through 1978 are shown by tag type (Table 1). A sufficient number of tag returns existed to allow examination of three separate recapture periods. Only a few returns existed from beyond the third recapture period. There were approximately equal numbers of each tag type released each year. Table 1 constitutes the basic data used throughout this study. Using the basic data, we estimated values of immediate (Type I) and instantaneous (Type II) shedding rates for each tag type. Further, we tested several hypotheses including: 1) equality of return rates for same year recaptures; 2) equality of return rates by estimated age; and 3) differences in returns and nonreturns over 2 or 3 yr time periods for various time intervals.

Using the double-tagging release data for all years combined (1971-77) the return rate for plastic tags was 5.1% the first year, 8.6% the second year, and 1.6% the third year. The return rate for metal dart tags was 5.5% the first year, 9.1% the second year, and 2.9% the third year. Therefore, for both types of tags the return rates increased the second year and decreased the third year. This should be expected since tagging occurred at the end of the purse seine season for several of the release years studied. Chi-square tests (not cor-

TABLE 1.—Tag releases and returns from northwestern Atlantic bluefin tuna double-tag study. For each of $k = 1, 2,$ or 3 recapture periods the number of returns of double-tagged fish retaining both tags is n_{ddk} and those retaining only one tags is n_{dsk}. The average number of days-at-large for each period is t_k.

	Double-tagged releases		First-year returns			Second-year returns			Third-year returns		
Tag type	Year	Number	n_{dd1}	n_{ds1}	t_1 (days)	n_{dd2}	n_{ds2}	t_2 (days)	n_{dd3}	n_{ds3}	t_3 (days)
Plastic dart (D-tag)	1971	150	4	0	7.25	20	9	349.07	3	1	724.00
	1972	75	6	0	12.83	17	4	340.52	1	1	726.50
	1973	134	18	2	18.45	6	4	354.20	0	1	708.00
	1974	629	25	4	12.07	18	12	352.17	4	7	727.82
	1975	50	0	1	40.00	1	1	384.50	0	0	0
	1976	267	12	2	16.36	2	2	341.00	1	2	707.33
	1977	223	3	1	47.50	25	4	361.83	—	—	—
	Total	1,528	68	10	16.46	89	36	352.06	9	12	723.10
Metal dart (H-tag)	1971	162	4	1	18.60	10	9	358.63	2	3	724.80
	1972	77	0	1	11.00	9	11	343.55	0	1	740.00
	1973	131	12	5	16.88	1	3	373.25	0	2	720.00
	1974	666	28	2	10.97	40	13	358.57	15	11	703.19
	1975	58	1	0	43.00	4	5	339.11	2	0	687.50
	1976	271	23	3	23.08	6	0	311.00	0	4	759.25
	1977	228	8	0	36.00	24	2	365.19	—	—	—
	Total	1,593	76	12	18.76	94	43	354.71	19	21	712.48
	Grand total	3,121	144	22	17.68	183	79	353.44	28	33	716.13

rected for continuity) showed that there were no significant differences at the 0.01 level, with 1 degree of freedom, in return and nonreturn rates between tag types for fish at liberty for 1, 2, or 3 yr (Table 2). However, returns were significantly better at the 0.05 level for metal tags in the third year. Further, there was no significant difference at the 0.01 level in the first-year return and nonreturn rates between the two types of dart tag, whether comparing each year individually or comparing all years combined (Table 3).

We also tested for differences in return and nonreturn rates between age-groups. Fish were aged from unpublished length-age tables (Rivas[3]). Chi-square values for fish tagged at ages 1, 2, 3, and 4+, were not significant at the 0.01 level (Table 4). The results of the chi-square test indicated that tag types and ages could be combined.

Unweighted and weighted linear regression models were used to estimate immediate tag shedding rate ($1 - \rho$) and instantaneous shedding rate (L) (Table 5). The unweighted model for both tags combined yielded an estimate of immediate tag shedding ($1 - \rho$) to be 0.040 (0.042 for the weighted model). The overall estimate of the instantaneous rate of tag shedding (L) on an annual basis using the model was 0.205 (0.186 for the weighted model). (The annual rate analog for L from the unweighted model is 0.19.) Therefore, the results from each model were similar. We chose to use the unweighted results, which give a slightly higher $\hat{L}$ value. While results of the chi-square test indicated that tag types could be combined, estimates were also made for each tag type separately to

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TABLE 2.—Chi-square tests (df = 1) of equality of yearly return and nonreturn rates between double-tagged releases for 1971-77 combined, for $k = 1, 2,$ or 3 yr at liberty, using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags is n_{ddk} and those retaining only one tag is n_{dsk}.

	Plastic dart tags			Metal dart tags			
Return year (k)	Double-tagged releases	Total returns kth year ($n_{ddk} + n_{dsk}$)	Return rate	Double-tagged releases	Total returns kth year ($n_{ddk} + n_{dsk}$)	Return rate	Chi-square value
1	1,528	78	0.05105	1,593	88	0.05524	0.272
2	1,450	125	0.08621	1,505	137	0.09103	0.213
3	1,325	21	0.01585	1,368	40	0.02924	5.452*
		Average	0.05104			0.05850	

*$P \leq 0.05$.

TABLE 3.—Chi-square tests (df = 1) of equality of return and nonreturn rates between double-tagged releases recaptured the same year using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags during the first year after release is n_{dd1}, and those retaining only one tag is n_{ds1}.

	Plastic dart tags			Metal dart tags			
Year	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Chi-square value
1971	150	4	0.02667	162	5	0.03086	0.049
1972	75	6	0.08000	77	1	0.01299	3.884*
1973	134	20	0.14925	131	17	0.12977	0.209
1974	629	29	0.04610	666	30	0.04505	0.008
1975	50	1	0.02000	58	1	0.01724	0.011
1976	267	14	0.05243	271	26	0.09594	3.699
1977	223	4	0.01794	228	8	0.03509	1.280
Total	1,528	78	0.05105	1,593	88	0.05524	0.272

*$P \leq 0.05$

TABLE 4.—Chi-square tests (df = 1) of equality of return and nonreturn rates by estimated age between double-tagged releases for all years 1971-77 combined, recaptured the same year, using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags during the first year after release is n_{dd1} and those retaining only one tag is n_{ds1}.

	Plastic dart tags			Metal dart tags			
Estimated age at release	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Chi-square value[1]
1	641	29	0.04524	647	31	0.04791	0.052
2	631	43	0.06815	656	43	0.06555	0.035
3	212	4	0.01887	226	12	0.05310	3.642
4+	44	2	0.04545	64	2	0.03125	0.148
	1,528	78		1,593	88		

[1] No values significant at $P \leq 0.05$.

TABLE 5.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for all years combined (1971-77) based on a 3-yr return period using unweighted and weighted linear regression models. (The weights used in the weighted model were equated to the ratio of the number of returns of double-tagged fish during each return period to the total number of returns of double-tagged fish during all periods.)

Model and tag type	$1 - \hat{\rho}$	$\hat{L}$ (annual)
Linear regression:		
Plastic dart	0.027	0.22886
Metal dart	0.049	0.19201
Combined	0.040	0.20452
Weighted linear regression:		
Plastic dart	0.033	0.19200
Metal dart	0.049	0.18213
Combined	0.042	0.18596

indicate the magnitude of the variances of the estimates.

Our estimate of $(1 - \rho)$ is slightly greater than the overall estimate of 0.027 given for bluefin tuna from the northwest Atlantic by Lenarz et al. (1973). The difference is small relative to the precision of the estimates. Our estimate of $(1 - \rho)$ for northwest Atlantic bluefin tuna is less than the value of 0.10 reported for Pacific yellowfin tuna by Bayliff and Mobrand (1972) and the value of 0.12 reported for North Pacific albacore by Laurs et al. (1976).

Our estimate of L is less than the overall estimate of 0.31 reported by Lenarz et al. (1973) for bluefin tuna and the L estimate of 0.278 reported for yellowfin tuna by Bayliff and Mobrand (1972). Our L estimate is greater than the estimates of between 0.086 and 0.098 reported for albacore by Laurs et al. (1976).

As previously noted, there was no significant difference in return rates found for the two types of dart tags for 1971-77. However, from examination of the data presented in Table 1, there appeared to be changes occurring in the shedding rates of each type of tag and a difference between the 1971-73 and 1974-77 time intervals. Therefore, we calculated $(1 - \hat{\rho})$ and $\hat{L}$ for each time interval and conducted chi-square tests (df = 6) for differences in returns over three recapture periods ($k = 3$) between time intervals and between tag types (Table 6). We found significant differences between time intervals for each of the tag types and significant differences between tag types for each of the time intervals. The plastic dart tags became less efficient, i.e., $\hat{L}$ increased over the time intervals, and the metal dart tags improved, i.e., $\hat{L}$ decreased over the time intervals.

TABLE 6.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for time intervals 1971-73 and 1974-77 based on a $k = 3$-yr return period. (A contingency table, 7 × 2, was constructed containing the number of double and single returns for each of the three recapture periods plus the number of nonreturns for each tag type and each time interval.) Results of chi-square tests (df = 6) for differences in double and single tag returns and total nonreturns between time intervals and tag types over a 3-yr recapture period are given.

Tag type and time interval	$1 - \hat{\rho}$	$\hat{L}$ (annual)	Chi-square value
Plastic dart:			
1971-73	0 029	0.14838	64.286**
1974-77	0.023	0.28455	
Metal dart:			
1971-73	0.140	0.37163	33.489**
1974-77	0.007	0.17242	
1971-73:			
Plastic dart	0.029	0.14838	18.924**
Metal dart	0.140	0.37163	
1974-77:			
Plastic dart	0.023	0.28455	18.135**
Metal dart	0.007	0.17242	

**$P \leq 0.01$.

The model of Chapman et al. (1965), which was modified by Bayliff and Mobrand (1972), assumes constant L over recapture periods. We decided to examine values of L over the two pairs of recapture periods $k = (1, 2)$ and $k = (2, 3)$ to determine how well our data fit the model. Since only two recapture periods were used, L and $(1 - \rho)$ were estimated by solving two simultaneous equations.

For the tag types and time intervals examined, there is an indication that $\hat{L}$ is not constant (Table 7). In fact, $\hat{L}$ increased in three out of four cases. The sequence of events could have happened due to chance alone, for if the changes in $\hat{L}$ came from a binomial distribution with $P = 0.5$, then the probability of $\hat{L}$ decreasing in three of the four cases or $\hat{L}$ increasing in three of the four cases is ≤ 0.25. However, $\hat{L}$ during the second time period is more than 60% $> \hat{L}$ in the first time period in three cases and only 16% $< \hat{L}$ in the first time period in the other case. While the data do not provide conclusive evidence that L is not constant, it would be dangerous to extrapolate beyond the time period used for analysis.

We previously noted that the 1974 releases were

TABLE 7.—Estimates of annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for 1971-73 and 1974-77 based on return periods of $k = (1, 2)$ and $k = (2, 3)$.

Tag type and time interval	Return period k	$\hat{L}$ (annual)
Plastic 1971-73	1, 2	0.16017
	2, 3	0.13421
Plastic 1974-77	1, 2	0.09925
	2, 3	0.45207
Metal 1971-73	1, 2	0.27858
	2, 3	0.45271
Metal 1974-77	1, 2	0.09331
	2, 3	0.24632

unique in that three individuals conducted the tagging operation, whereas only one individual tagged and released the remainder of the fish from the other years. Therefore, we analyzed the data from the time intervals 1971-73 and 1975-77 separately from the 1974 data. For the following reasons we decided to examine only two recapture periods, $k = (1, 2)$: 1) 1977 has only two recapture periods possible (Table 1); 2) the number of single as well as double returns for $k = 3$ for both 1971-73 and 1975-77 constitutes very small sample sizes (Table 1); and 3) L appears to have been changing over $k = (1, 2)$ to $k = (2, 3)$ (Table 7).

Our analysis showed (Table 8) that there was a significant difference in return and nonreturn rates between time intervals for each type of dart tag. Also a significant difference in shedding rates was found between the plastic and metal type tags during the time interval 1971-73. A small sample size may account for the lack of a significant difference in shedding rates for each type of tag during the time interval of 1975-77. There also was no significant difference found in the shedding rates between each tag type during 1974. As previously mentioned, fish were released under different circumstances during 1974. During the 1971-73 time interval, plastic tags were found to be superior. We again found that the metal tag improved (Table 8), i.e., $\hat{L}$ decreased, between 1971-73 and 1975-77. Also, $\hat{L}$-values for the plastic tag decreased, but results yielded a negative value for the 1975-77 time interval, which is theoretically impossible and is due to variability in the data.

TABLE 8.—Estimates of immediate $(1 - \hat{p})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for 1971-73, 1974, and 1975-77 based on a k = 2-yr return period. (A contingency table, 7 × 2, was constructed containing the number of double and single returns for each of the three recapture periods plus the number of nonreturns for each tag type and each time interval.) Results of chi-square tests (df = 4) for differences in double and single tag returns and total nonreturns between time intervals and tag types over a 2-yr recapture period are given. (Results for the period 1971-72 from Lenarz et al. (1973) are shown for comparison.)

Tag type and time interval	$1 - \hat{p}$	$\hat{L}$	Chi-square value
Plastic dart:			
1971-73	0.028	0.16017	39.460**
1975-77	0.118	<0.	
Metal dart:			
1971-73	0.169	0.27858	22.186**
1975-77	0.114	0.05860	
1971-73:			
Plastic dart	0.028	0.16017	17.323**
Metal dart	0.169	0.27858	
1974:			
Plastic dart	0.067	0.22615	8.318
Metal dart	0.031	0.12126	
1975-77:			
Plastic dart	0.118	<0.	6.636
Metal dart	0.114	0.05860	
1971-72:			
Plastic dart	0.000	0.21615	
Metal dart	0.099	0.26278	

**$P \leq 0.01$.

From our analysis, we cannot conclusively show that one of the two types of dart tags is better for bluefin tuna tagging. Both tag types appeared to improve between 1971-73 and 1975-77. Plastic tags were significantly better than metal in the first period and nonsignificantly better in the second.

We have shown that tag shedding rates vary from 1 yr to another. There are some possible reasons for the observed variability. One reason may be changes in tag design or quality. To our knowledge there was no intentional effort made by the manufacturers to change the design of the metal or plastic dart tags used in this study. A different type of glue, however, was used during 1972 through 1977 for the plastic dart tags. Before using the plastic dart tags, we tested them by pulling on the barb. On several occasions, we discovered that the barbs were not adequately secured. We reglued these tags before using them. We also examined the metal dart tags prior to their use. In general, they appeared to be trouble free. Several orders of both types of tags were used during the course of this study. We were unable to correlate changes in the shedding rates with the specific batch of tags that were used. The shelf life of the plastic used in the tags may be another factor. In some instances we used tags which were manufactured several years before their actual use. Since there were no changes in the tagging method, this reason was discounted. Tagging occurred throughout the purse seine fishing season during 1971, 1973, and 1974, and at the end of the season during 1972, 1975, 1976, and 1977. We do not see why this would have more of an effect on one type of tag than on the other.

Summary and Conclusions

Return data for double-tagged northwestern Atlantic bluefin tuna were used to estimate the shedding rates of plastic and metal dart tags. No significant difference was found between the return rates of the plastic and metal tags when the data were tested for all years combined, but plastic tags appeared to have lower shedding rates than metal tags in most cases. We believe that the combining of the data of all years together (1971-77) probably yields a reasonable approximation to the average shedding rate for each type of tag. Type-I shedding, which occurs immediately after release, was estimated to be 0.040 for plastic and metal dart tags combined. Type-II (instantaneous) shedding was estimated to be 0.205 for plastic and metal tags combined on an annual basis.

The shedding rates for each type of tag were found to vary over the time period studied, and deviations from the assumption of constant shedding throughout the life of the tagged fish were noted. Due to these differences, one should not be satisfied with the results of one double-tagging experiment. We recommend that double tagging be employed whenever possible, as long as shedding occurs and the rate of shedding is found to vary. Also, tagged fish, especially the ones which have been at liberty for a long time, are more likely to continue to carry at least one tag if they were originally double tagged. The ones that do not continue to carry at least one tag are of no value. Furthermore, relative to the errors inherent in a study of this type we do not feel that there is really any important difference in shedding rates between the plastic and metal dart tags.

Since shedding may increase with time from release, extrapolations based on the assumption of constant L should be made with caution. Also because the tag shedding rates that we found are considerable, efforts should be made to develop a more efficient type of tag with a lower rate of shedding.

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INFLUENCE OF LITTLE GOOSE DAM ON UPSTREAM MOVEMENTS OF ADULT CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

A major environmental and economic concern in the Pacific Northwest is the continuing decline in the numbers of Columbia and Snake River salmonids. Several investigators (Johnson 1960 and others) have used biotelemetry to study effects of hydroelectric dams (Figure 1) on the upstream movements of adult salmonids. Results indicated upstream movements were delayed at Bonneville (Schoning and Johnson[1]; Monan and Liscom[2,3,4,5]),

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ENVIRONMENTAL INPUTS TO FISHERY POPULATION MODELS FOR EASTERN BOUNDARY CURRENT REGIONS

Andrew Bakun[1] and Richard H. Parrish[1]

ABSTRACT

Methods for incorporating information on environmental variation in fishery management models are not presently well developed. Rational approaches are hindered by lack of detailed knowledge of the linkages between environmental fluctuations and their effects on fish stocks. Empirical approaches are limited by lack of sufficient data points.

Recent advances have been fostered by the development of several promising hypotheses based on laboratory and field experiments and on comparative studies of geography and seasonality of spawning strategies. In addition, time series indicators of the important environmental processes involved in these hypotheses are becoming available. A review of developments concerning environmental effects on recruitment in a number of California Current stocks is presented.

The state of the art in the production of fishery-environmental indicator time series for eastern boundary current regions is surveyed. Fishery modeling is discussed from the points of view of rational models of the early life history and juvenile stages and of empirical models based on data from the post-recruit stage. In these post-recruit models, early life history and juvenile processes are incorporated by means of empirical stock-recruitment functions which may contain environmental dependencies.

Further progress is anticipated through laboratory and field experiments, dynamic process models, and seasonal-geographical comparative studies. Newly-developed techniques for aging of larvae promise dramatic increases in data on larval survival processes. It is pointed out that the four major eastern boundary current regions of the world, i.e., the Canary, Benguela, Peru, and California Current regions, involve similar environmental dynamics and contain very similar assemblages of economically-important fish stocks; inter-regional comparative studies are advocated.

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INTRODUCTION

Recent precipitous declines in important fishery stocks around the world have pointed out an urgent need for advances in fishery management science. A particular need is for realistic models which can predict and simulate effects of various management options. In most existing management models, the surplus production of a stock is assumed to be a relatively constant function of stock size. Recent events have shown this assumption to be inadequate under conditions of environmental perturbation.

Properly incorporating environmental effects in fishery models can be a difficult problem. There are two basic approaches: (1) the rational (cause-effect) approach which is based on an understanding of the physical and biological processes involved, and (2) the empirical approach in which the functional relationships are defined by analysis (by means of statistical regression, etc.) of available data.

A strictly rational approach is usually not feasible. The complex linkages between environmental processes and biological consequences are incredibly difficult to observe or to investigate experimentally; the quantitative information needed to construct rational models of those linkages is most often unavailable. On the other hand, the empirical approach is hampered by a chronic lack of sufficient data points. Fishery data characteristically yield one estimate of stock size or recruitment per year; the available time series generally does not exceed several decades and most often is of the order of 10 to 20 years. To sort out a multitude of possible environmental effects by statistical means from a series of 10 to 20 data points is not possible. Moreover, the time series often contain significant autocorrelation, indicating a lack of independence of data points, which further depletes the severely limited degrees of freedom.

Generally, a combination of the two approaches allows the greatest amount of available information to be incorporated. The rational approach is used to generate hypotheses and to test and quantify those processes which can be measured or addressed experimentally. Then the empirical approach is used for testing, verification, and calibration. The demarkation between the two approaches is important. Often in fishery science an hypothesis is generated on the basis of experience, and since rational explanations can be constructed (because of the multitude of possible interacting processes occurring in marine biological communities it is nearly always possible to find a rationalization for any empirical result) the hypothesis comes to be regarded as rational when in fact it is basically empirical. Then when the hypothesis is "tested" against the time series of available data, which nearly always contains the period of experience which generated the hypothesis, a "verification," not surprisingly, is indicated. When basically the same data is used to test a hypothesis as was used to formulate it, obviously no real test can occur. For this reason many published fishery-environmental "relationships" are in reality untested hypotheses; it should not be surprising that they often fail almost immediately after publication.

Even when there is considerable rational input available, it is necessary to limit the choices of explanatory environmental variables to minimize the chances of spurious "fits" to the very limited time series. Thus as much rational input as possible must be utilized in formulating pertinent environmental indicators. In the past, measured environmental properties have often been used to produce correlations with fishery data in the belief that the same environmental processes which alter the measured properties would also alter the fish stock parameters. However, the linkages between the environmental processes and the observed properties may be just as (or more) tenuous and subject to independent alteration, as those between the processes and the biological consequences of interest. Certainly, a property is easier to measure than is a process, and a property has the reassuring attribute of having a single scalar value at a given point in space and time. In addressing a process one must come to grips with a space - time continuum in which a choice of scale is critical. However, due to the lack of any excess degrees of freedom to deal with additional linkages it is advisable to focus as directly as possible upon the actual involved processes in formulating environmental variables for fishery modeling efforts.

Recently several promising rational hypotheses concerning environmentally-caused recruitment variation in fish stocks of eastern boundary current regions have appeared. (1) A sensitivity of reproductive success of pelagic fish stocks to the dissipation of fine-scale food strata by wind mixing during early larval feeding (Lasker, 1975, 1978) has been indicated through a remarkable series of laboratory and field experiments. (2) A detrimental effect on coastal fish stock of offshore transport during the larval drift period has been suggested by comparative studies (Parrish, Nelson and Bakun, MS) of the seasonal and spatial characteristics of reproductive strategies and drift conditions in the California Current region. (3) Since it is generally thought that the massive fish stocks inhabiting eastern boundary current regions depend on the primary production supported by the vigorous coastal upwelling characteristic of these regions, it is expected that long time scale fluctuations in upwelling intensity would be linked to fish stock variations.

The four "classical" eastern boundary currents (Wooster and Reid, 1963) are the Canary Current off the Iberian Penninsula and northwestern Africa, the Benguela Current off southwestern Africa, the Peru Current off western South America, and the California Current off western North America. These also comprise the four main upwelling regions of the world, as cited by Cushing (1969). They are characterized by rather broad, slow equatorward flow, high primary productivity, and massive pelagic fish stocks which have experienced extreme fluctuations. Very similar assemblages of fishes appear to constitute the major portion of the exploitable biomass in all four regions. In each, there is an anchovy, pilchard (sardine), horse mackerel (jack mackerel), hake, mackerel and bonito. The species are very closely related and several of the species are found in more than one region (Table 1). The similarity of the pelagic fish community in the eastern boundary currents suggests that the processes occuring in these systems may be direct analogs. It is possible that the environmental processes which regulate the recruitment and population fluctuations of a species group, for example the anchovy (*Engraulis*), are similar in all of the eastern boundary currents.

TABLE 1. Dominant anchovy, pilchard, horse mackerel, hake, mackerel and bonito in the four major eastern boundary currents.

CALIFORNIA CURRENT	PERU CURRENT	CANARY CURRENT	BENGUELA CURRENT
Engraulis mordax	*Engraulis ringens*	*Engraulis encrasicholus*	*Engraulis capensis*
Sardinops sagax	*Sardinops sagax*	*Sardina pilchardus*	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus symmetricus*	*Trachurus trachurus*	*Trachurus trachurus*
Merluccius productus	*Merluccius gayi*	*Merluccius merluccius*	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*	*Scomber japonicus*	*Scomber japonicus*
Sarda chiliensis	*Sarda chiliensis*	*Sarda sarda*	*Sarda sarda*

DEFINITION OF ENVIRONMENTAL VARIATION

If fishery environmental studies are to lead toward management systems which are capable of adapting to environmental variations, the data required to indicate these variations must be of a type that can be obtained on a continuing basis. Thus, it is advantageous to base these studies on the sort of data that are routinely gathered, or that can be obtained by a minimal survey effort.

Generally, the physical characteristics of the environment which are thought to have important effects on recruitment variations can be grouped into four major categories:

1. The field of horizontal advection,

2. The field of vertical stability,

3. The field of temperature,

4. The field of convergence and divergence of flow at the sea surface, which is linked to the field of vertical advection.

In addition there are available certain physical indicators which are sometimes considered as "integrators" of several (or many) environmental effects.

Horizontal advection

Biological processes in the sea tend to integrate very short-scale variations in the physical environment. For instance, in the case of transport of planktonic fish eggs and larvae, since spawning generally is distributed in time and space, and eggs and larvae may passively drift for an extended period, short-scale flow variations tend to be averaged out by the space-time continuum of drifting organisms (Parrish, et. al., MS).

On large time and space scales, flow in the ocean is well approximated as a simple combination of the geostrophic current field and the field of Ekman drift induced by the horizontal force exerted by the wind on the sea surface (Greenspan, 1968). The conceptual picture, therefore, is of a thin surface layer of Ekman wind drift which varies in phase with large-scale atmospheric weather patterns, superimposed on the deeper, more slowly varying geostrophic flow field. The Ekman layer is thought to extend no deeper than 50 to 100 meters below the sea surface, and most of the transport probably occurs in the upper 5 to 30 meters.

The geostrophic current at the sea surface is directly proportional to and at right angles to the slope of the sea surface. The constant of proportionality is a function of latitude, being a minimum value at the poles and increasing to an infinite value at the equator; thus the geostrophic approximation is useless directly on the equator but Montgomery and Stroup (1962) have indicated it to be a useful estimate of current velocity as near as several degrees of latitude to the equator.

The standard method for estimating the sea surface slope is by measuring the temperature and salinity of the ocean at various depths, thereby determining the field of density of the sea water. For water to be motionless at some deep level there must be no horizontal variation in the weight of the water column pressing down from above. Thus, the horizontal differences in thickness of the column, and thereby the sea surface slope, can be computed from the internal density field (Sverdrup, et. al., 1941). Although there is probably no level at which the ocean is completely motionless, the geostrophic velocities at great depths tend to be much smaller than those at the surface, and so this method provides an acceptable approximation.

Surveys using this method have been made in all the major eastern boundary current regions. In the California Current, the CalCOFI surveys have made regular observations since 1949. The flow patterns described are quite detailed. However, methods for applying this wealth of detail to biological problems are not well worked out; as yet, little use has been made of these data in explaining biological variations. Such surveys are expensive, and obtaining the required space-time continuity of coverage is a problem.

For some purposes a schematic picture of the normal seasonal variation of geostrophic flow is required. This is not necessarily easy to get. Simple averages of the few available samples of sea surface topography as done by Wyllie (1966) and Hickey (1979) can be dominated by atypical features. This procedure can also introduce spurious features that never occurred in any of the measured samples. For example, during a particularly warm year the sea surface would tend to stand higher than normal throughout a given region; this would not generate any current features since currents are related to the gradient of surface height. Since spatial coverage is seldom complete in any one year, if observations from the warm year are averaged with those from several more normal years, the locations containing data from the warm year would tend to be higher than other locations. The surface slopes thus generated would determine current patterns that never actually existed.

Parrish, et. al. (MS) used the long-term mean temperature and salinity summaries produced by Robinson and Bauer (1973) to produce a smoothed long-term mean geostrophic pattern for the California Current region in which atypical features are suppressed; however, lack of indication of the typical seasonally varying features is a major deficiency. Because temperature observations are much more numerous than salinity observations, Husby[2] has produced some interesting seasonal patterns by combining

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2. Personal communication, David M. Husby, Pacific Environmental Group, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Monterey, California, 93940.

seasonal temperature fields with long-term mean salinity fields. Other approaches include the association of non-observed salinity values with observed temperature values through the use of a characteristic temperature-salinity (T-S) relationship (Emery, 1975) and the filling of data gaps by curve fitting to existing data points by harmonic analysis[3].

An ideal situation is where the sea surface slope variations can be directly measured; the long-period variation in the difference in measured sea height between two sea level gauges on either side of an ocean current is directly proportional to the variation in the space-averaged geostrophic surface flow across a line drawn between the two gauge locations. Saur (1972) produced a very large space scale index of monthly variations in geostrophic surface flow between sea level gauges located in San Francisco and in Honolulu. Christensen et. al. (1979) used sea level differences between Guadalupe Island and the coast of Baja California to indicate flow variations on a scale which is probably more pertinent to coastal fish stocks. Wyrtki (1974) showed that an array of sea level gauges on tropical islands could successfully monitor changes in the equatorial current system of the Pacific.

In most cases there exists no convenient island located the proper distance offshore to indicate flow variations on a scale upon which they would be affecting fish stocks. In these cases it may be reasonable to assume that the largest sea level variations will be at the solid coastal boundary and thus that a single coastal sea level station can be an index of major alongshore geostrophic flow variations. The most likely offshore length scale to be involved in such an index is the baroclinic Rossby radius of deformation (Mooers and Allen, 1973) which is of the order of 10 to 20 km in the subtropical eastern boundary current regions. For example, Smith (1974) and Reid and Mantyla (1976) found correspondence of coastal sea levels at certain California Current locations with measured variations in alongshore flow. Marthaler (1976) indicated that the monthly mean near-surface currents over the Oregon continental shelf could be estimated from a regression with coastal sea level to a precision of ± 6 cm/sec where the annual range is 60 cm/sec. Off the New England coast of the eastern North America, where the continental shelf is relatively wide, Beardsley and Butman (1974) found that, if they assumed a constant sea level at the shelf break, a coastal sea level measurement could indicate the alongshore geostrophic flow (averaged over the shelf width) to ± 15%.

Sea level measurements are available in long time series in all the major eastern boundary current regions. The Permanent Service for Mean Sea Level[4] lists monthly mean values for the California Current since the turn of the century (e.g., San Francisco since 1897, San Diego since 1906), nearly as long for the Canary Current (Lagos since 1908, Santa Cruz de Tenerife since 1927), for the Peru Current since the early 1940's (eg. Matarani since 1941, Talara since 1942) and for useably long time series for the Beneguela Current region (eg. Walvis Bay, 1958-72). Sea level time series are subject to distortion by geological uplifting and downwarping of coastal regions but these are usually of much longer time scale than the fishery variations of interest, and so can be easily corrected by linear or first-order curvilinear detrending, or by low-pass filtering. Sudden discontinuities due to earthquakes, etc., are usually well documented.

The other major component of flow, the surface wind-induced Ekman drift, which combines with the geostrophic flow to determine the actual water movement in the ocean surface layer, presents a different sort of problem. It cannot be inferred from any signal that is measured within the ocean and varies rapidly, adjusting to wind variations on a time scale of less than a day (except very close to the equator). It can be estimated from the field of wind stress on the sea surface. This stress field must be constructed from scattered reports from ships at sea and from observations at coastal stations which may be distorted by effects of local land topography. Because of the rapid variation, frequent sampling is required, preferably at intervals of twelve hours or less. Standard reporting periods have been established by international convention to provide synoptic samplings which are disseminated globally. These are arranged into consistent analyzed fields by various national meteorological agencies, commonly at 6-hourly, or even 3-hourly intervals.

[3] Method developed by Ronald J. Lynn, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92037.

[4] Institute of Oceanographic Sciences, Bidston Observatory, Birkenhead, Merseyside L43 7RA, England.

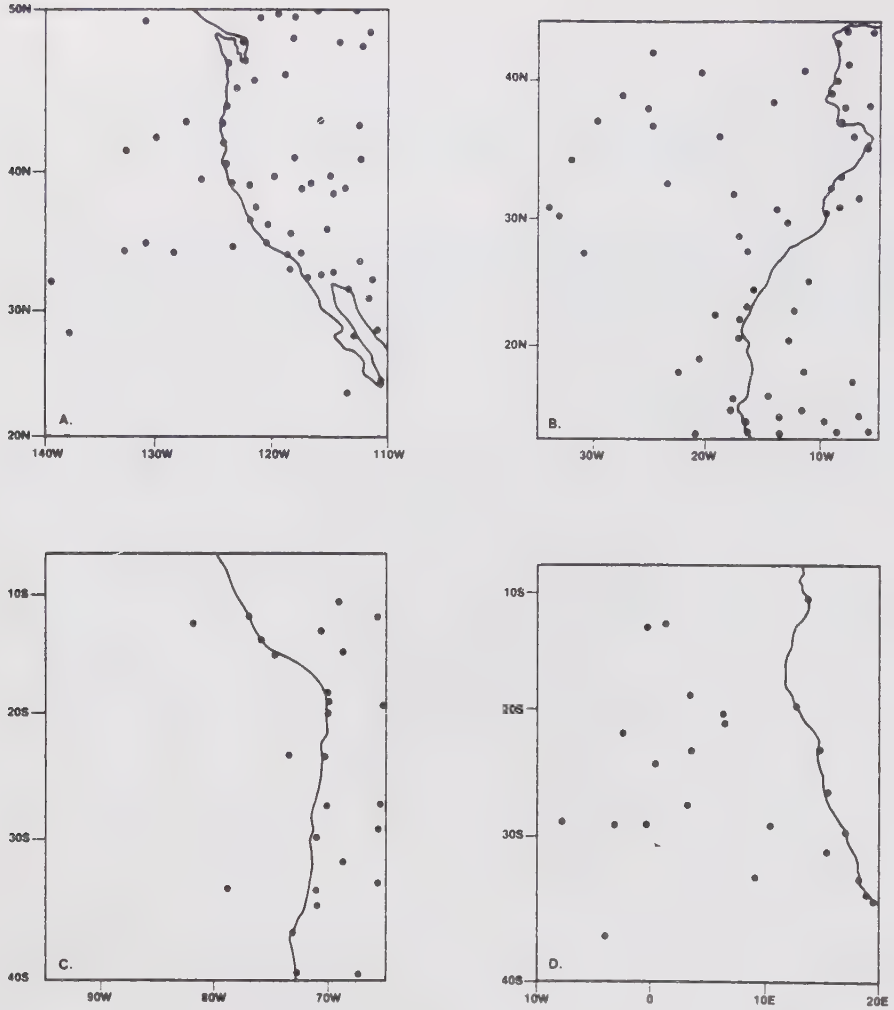


Figure 1. Typical synoptic report distributions in the four major eastern boundary current upwelling regions: A. the CALIFORNIA CURRENT (distribution shown is for 0600 GMT, Jan. 11, 1980), B. the CANARY CURRENT (0000 GMT, Feb. 12, 1980), C. the PERU CURRENT (1800 GMT, Feb. 7, 1980), and D. the BENGUELA CURRENT (1900 Gmt, Feb. 7, 1980).

The report density available in any synoptic sampling for any of the major subtropical eastern boundary current regions does not normally exceed several per 5-degree latitude - longitude "square" (Figure 1). In order to form consistent time series from such sporadic report distributions, it is necessary to spread the large-scale information represented in the observations to consistent geographical locations and to suppress measurement and transmission errors and small-scale information which is nonrepresentative of the large-scale. The analysis procedures used by meteorological agencies to prepare synoptic data fields for forecast purposes are designed to accomplish these same results, and thus provide a resource for the production of sea surface wind stress time series. Many of the standard analysis procedures (e.g. Holl and Mendenhall, 1972) are designed for use in temperate latitudes and make use of the strong geostrophic coupling between wind and atmospheric pressure distributions to employ both types of observations and thereby increase the data base. In the tropics, where the geostrophic coupling becomes weak these methods do not work well. However, there are certain analysis procedures designed specifically for the tropics (e.g. Lewis, 1972) which are in routine use at the present time.

Once an estimate of the wind field over the sea surface is available it can be readily converted to an estimate of the surface Ekman transport field in the ocean. However it is important to note that the linkage of wind velocity to wind stress is non-linear. Thus, where time averages are to be made, the averaging should be performed after the stress computation. Bakun (1973) has shown that time series of monthly alongshore stress estimates computed from monthly mean winds at locations near the west coast of North America correlate highly with corresponding series of monthly means of synoptic stress computations. The high correlation is probably due, at least in part, to the effect of coastal topography in constraining the directional variation of the wind. Thus, although it seems likely that similar high correlation would occur in other eastern boundary current regions with coastal mountain ranges, it remains an untested assumption. In regions where the directional variance of the wind is high, in the mid-latitude central ocean, for example, such an assumption is probably unwarranted. Bakun (1973, 1975) has discussed certain other problems in using analyzed atmospheric fields near coastal boundaries.

A major unsolved problem is the assignment of "error bars" to the stress estimates computed from atmsopheric analyses. The estimates appear to be quite adequate for defining variations on the energetic "synoptic atmospheric event" and "seasonal" scales, and to identify major interyear differences. However, their adequacy in defining subtle differences among groupings of years remains undemonstrated.

Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter and is directed 90° degrees to the right (left) of the stress in the northern (southern) hemisphere. The fine-scale vertical structure of the Ekman drift velocity field depends on vertical eddy viscosity characteristics which are not well known; however the total transport of water in the layer between the sea surface and the depth at which the drift velocity becomes negligible does not depend on these characteristics, and can be inferred from the wind stress alone. The depth of negligible Ekman drift velocities is likewise not well known. However, as mentioned above, most of the transport probably occurs in the upper 20 to 30 meters. It is unlikely that appreciable Ekman drift would penetrate below the surface mixed layer into the stratified portion of the water column. Aggregates of organism's which are continually being mixed over a depth range as deep as or deeper than the Ekman layer can be assumed to move with the Ekman transport; in this case a drift speed can be assigned by dividing the Ekman transport by the depth of mixing.

The upper portion of the Ekman layer would tend to move at a lesser angle to the direction of the wind stress. Classical Ekman theory, assuming a constant vertical eddy viscosity, predicts the free ocean surface to move at an angle of 45° to the wind. An analysis by Madsen (1977), in which he assumes an eddy viscosity varying linearly with depth, yields a surface deflection of about 10°. Empirical studies reported by Stommel (1954) found speeds of drift at the sea surface to be of the order of 1/20 to 1/30 of the wind speed, with deflection angles usually between 30° and 60°.

Detailed specification of the vertical distribution of Ekman velocity is not available. The classical Ekman spiral is not generally observed. The interaction of Langmuir-type circulations (Scott, et. al., 1969), etc., is not well understood. However, we can be quite certain that the Ekman transport concept is realistic, at least in a time- and space- average sense, both from dynamical necessities (Greenspan, 1968) and from climatological correspondences of wind and oceanic distributions (e.g. Wooster and Reid, 1963; Wooster, Bakun, and McLain, 1976). For fisheries applications, it appears necessary to make do with the concept of Ekman transport, modified by a somewhat vague notion that the very surface moves at an angle more directly downwind than does the depth-integrated transport. At the equator the Coriolis parameter goes to zero and so the Ekman transport relationship "blows up"; the evidence of equatorial divergence of ocean surface waters indicates some degree of Ekman effect acting even very near the equator.

Direct measurements of ocean flow cannot generally provide the required time and space coverage required for operational fishery management purposes. One type of direct measurement which has been useful in climatological studies of eastern boundary currents (Wooster, et. al., 1976; Bakun, et. al., 1974; Bakun and Nelson, 1977; Bakun, 1978) is the so-called "ship drift" observation. These are differences, attributed to ocean currents, between dead-reckoning and verified positions as recorded in ships log books. These have been gathered since the last century and have provided the basis for much of our knowledge of large scale ocean currents. The data contain a very large error variance, being based on differences between rather uncertain navigational fixes, estimates of ship speed, etc., and require a very large sample to achieve a meaningful estimate of mean current speed. Although observations are rejected when wind speeds are very high, the data are undoubtedly contaminated by the effects of wind on the ships superstructures. The data appear adequate to define long-term mean seasonal variations, but are not numerous enough to be useful in indicating interyear variability.

Vertical Stability

Recent work (Lasker, 1978) has indicated extreme sensitivity of anchovy reproductive success to the breaking up of fine-scale food strata by wind mixing during early larval feeding. We can estimate variations of wind mixing energy added to the water column from available analyzed wind fields; the energy added varies in rough proportion to the cube of the wind speed (Elsberry and Garwood, 1978). The stability of the upper water column, which would oppose such mixing might be estimated from vertical temperature and salinity structure. Little is known concerning the time scales of aggregation of food strata or the ability of the food organisms to themselves resist dispersion by turbulence. It is difficult to formulate a proper index of the wind effect in this case. A first impulse is to look at interyear variations in the cube of the wind speed averaged over a spawning season as the relevant factor. However, it probably is not the average intensity that is critical, but the existence of sufficient time-space "windows" within which wind-induced turbulence does not exceed a certain critical value. We do not know what the critical value is and we do not know the length of time required for formation of the food concentrations needed for successful first feeding of larvae. This appears to be a very fruitful ground for research. Application of recent advances in oceanic mixed layer modelling should be helpful in determining at what point turbulence would be initiated. Repetitive samplings of biological microstructure under varying wind conditions would begin to define time scales of aggregation and ability to resist dispersion. Perhaps comparative studies of conditions in areas where fish normally spawn (i.e. favorable to larval survival by natural selection), as opposed to conditions in areas where spawning does not occur, would yield some information on normal requirements for reproductive success. Such information might then be used to define a formulation to correctly indicate the effect on year-class success of interyear variations in wind-induced turbulence.

Temperature

Sea temperature is probably the most commonly used environmental variable in studies of biological variations. There are several reasons for this. Probably most important is that temperature has a direct physiological effect. The rates of biological processes increase and decrease with temperature, and extremely unfavorable temperatures can be lethal. Thus, temperature can define limits of occurrence; anomalous temperature conditions, by changing growth and maturation rates, can cause disruptions and mismatches in the timing of critical life cycle events. Of perhaps nearly equal importance is the availability of temperature data, due in some extent to the simplicity and ease of the measurement. Finally, temperature provides a signal of important ocean processes; for example in eastern boundary current regions, cool sea surface temperatures are often related to coastal upwelling or to horizontal advection from higher latitudes.

Sea surface temperature is routinely measured and reported by ships at sea. The observations are distributed internationally through the World Meteorological Organization (WMO). Subsurface temperature observations are much less plentiful, but these are also gathered and distributed by WMO and the Intergovernmental Oceanographic Commission (IOC) through the IGOSS program. Sea temperature is also routinely measured at many coastal stations. These observations have the advantage of being a generally continuous time series at a consistent location. They are sometimes subject to very local influences, often being located in or near harbors and estuaries. Temperature signals from coastal stations located within a region occupied by a single fish stock can exhibit a disconcerting degree of noncorrelation.

This brings up the problem of how to choose from a variety of available temperature signals in attempting to define a useful relationship to biological events. The procedure of searching a number of possible signals to find the "most pertinent" one, i.e., the one that yields the best correlation, and then applying a standard significance test to the regression results in a misleading overestimate of significance. After all, a 95% significance level signifies only that the chance of an equivalent degree of correlation from unrelated random series is one in twenty. Thus if one tests four unrelated series the probability of finding a correlation significant at the 95% level is increased to one chance in five, corresponding to an 80% significance level which may be inadequate to confidently reject a null hypothesis of no relationship.

Various methods are employed to summarize scattered temperature observations to produce time series indicative of conditions in the environment. None should be used blindly. The space scales of temperature variation in the ocean may be quite small and not well sampled by the available distribution of observations. Thus the variation in distribution of reports may introduce spurious variability capable of obscuring the true variation. Averaging by areal segments of the ocean surface (e.g. McLain, 1978) can be a particular problem in coastal upwelling regions where horizontal temperature gradients are large.

Use of meteorological-type "objective analysis" procedures (e.g. Laevastu and Hela, 1970), where available data is spread to areas where data is lacking, may involve similar time series distortions. Often climatology is used in these procedures to fill large space-time data gaps. The resulting time series can be difficult to interpret; methods for establishing error limits are not available.

Recently there has been widespread use of empirical orthogonal function (or principal component) analysis in studies of climatic fluctuations (Preisendorfer, 1977). In this way temperature series from several locations can be combined into a single series, based on the linear combination which explains the largest fraction of the total variance of the individual series (Weare, Novato, and Newell, 1976). These techniques have not yet been widely used in fishery studies. They can probably be useful if properly employed. However, there should always be a firm physical basis for believing that the linear combination which contains the most variance is a more pertinent indicator of the effect upon the biological process of interest than is some other possible combination. Otherwise, one is simply adding another time series to a situation in which the major need is to limit the choices of explanatory series so that the concept of statistical significance can be meaningful.

Convergence, divergence, upwelling

An important aspect of the surface Ekman drift is that it is subject to strong convergences and divergences, convergence being a net gain of surface water at a point due to spatial gradients in horizontal transport, and divergence being a net loss. Thus sinking waters are generally found immediately below surface convergences, and rising waters below divergences.

Floating organisms would tend to be concentrated in areas of convergence and dispersed in areas of divergence. The rising waters in areas of divergence can aid non-motile phytoplankton in remaining in favorable light intensities for photosynthesis. Rising deeper waters replenish exhausted nutrient concentrations at the surface and cool the surface layers. Spatial gradients in surface convergence or divergence can tilt the subsurface density structure and establish sea surface slopes which alter the underlying geostrophic current field. Thus convergence and divergences in the surface wind drift affect the biological environment in a variety of ways and on a variety of scales; variations in the wind stress at the sea surface are probably the major external driving forces leading to biological perturbations.

The strongest convergence and divergence can occur next to a coastal boundary where transport gradients essentially reflect a step increase from zero on the continent to a finite value in the ocean. Where the surface transport adjacent to the coast is directed offshore, the result is locally wind induced coastal upwelling. Bakun (1973) produced time series estimates of monthly variations in the onshore-offshore component of Ekman transport. These were called "upwelling indices" (after Wooster and Ried, 1963) to call attention to the fact that, lacking direct measurements of coastal upwelling intensity, the variations in the local driving force, the alongshore wind stress, may be the best available indicator of upwelling variations.

Recent research has indicated the likelihood of poleward propagation of upwelling characteristics. This appears to be less important, at least on the seasonal scale, in the higher latitude eastern boundary current upwelling regions (Smith, 1974; Bakun, et. al. 1974; Wooster, et. al. 1976) than in the lower latitude regions, for example, the Peru (Smith, 1978) and Guinea (Bakun, 1978) coasts. However, even in Peru, Smith (1980) finds that the onshore-offshore component of flow is well represented by the locally wind-induced Ekman transport.

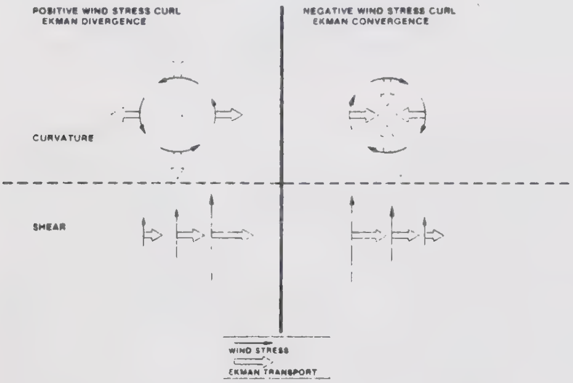


Figure 2. Wind stress curl and resulting Ekman transport. Positive curl expresses the anticlockwise (cyclonic) rotation due to either curvature or shear in the wind field; since the Ekman transport is directed perpendicularly to the right of the stress the result is Ekman divergence in either case. Negative curl expresses the clockwise (anticyclonic) rotation in the field; the result is Ekman convergence.

The onshore-offshore scale of the coastal divergence is related to the baroclinic Rossby radius of deformation (Mooers and Allen, 1973) which is of the order of 10 to 20 km in subtropical regions, although features of the continental shelf topography may, under certain circumstances, cause seaward expansion of this scale (Huyer, 1976). Offshore of this coastal boundary region, the convergence and divergence of surface Ekman drift is controlled by the wind stress curl (Fofonoff, 1963), which is a measure of the "rotation" in the wind field represented by curvature or shear (Fig. 2). Monthly surface layer divergence indices based on wind stress curl estimates were proposed by Bakun and Nelson (1977). The problem of establishing expected error bars on these estimates is even more bothersome in this case than in the case of Ekman transport indices since the process of taking derivatives amplifies errors. This problem is presently unsolved and the significance of computed wind stress curl anomalies is uncertain at this point. However, Chelton (1980) has reported a significant relationship between wind stress curl variations computed in this manner and low frequency variations in the onshore-offshore contrast in flow of the California Current, i.e., the tendency for the flow to be less southward (more northward) near the coast than in the offshore region.

The coupling of the surface convergence or divergence associated with the coastal boundary with that occurring offshore of the boundary zone presents possibilities for various combinations (Fig. 3) of probable biological significance. For example, a situation of coastal upwelling with negative wind stress curl causing offshore convergence (Fig. 3(d)) would favor concentration of drifting organisms upon being transported out of the coastal upwelling zone. This particular situation appears to be typical of the central Baja California upwelling center (Bakun and Nelson, 1977).

The effect of such couplings on the geostrophic current pattern can apparently have biological consequences. For example, the negative curl area off central Baja California corresponds to an apparent "blocking" of northward counterflow along the coast during the fall relaxation of upwelling-induced southward circulation (Bakun and Nelson, 1977). Semi-independent gyral circulations occur in the positive curl regions to the north and south (Fig. 4). These correspond to the areas of occurrence of separate subpopulations of California Current pelagic fishes including sardine (Clark, 1947), Pacific mackerel

(Roedel, 1952) and northern anchovy (Vrooman and Smith, 1971). This suggests the possibility that fluctuations of the wind stress curl pattern could influence exchanges between subpopulations. Indeed, Parrish and MacCall (1978) find variations in the wind stress curl in the region of separation to be significantly related to recruitment variations in the Pacific mackerel stock to the north.

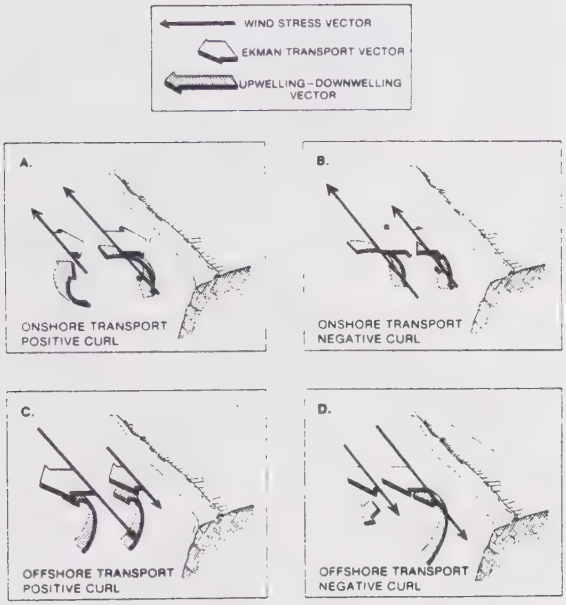


Figure 3. Types of couplings between surface convergence or divergence at the coast (due to the onshore-offshore component of Ekman transport) and that (due to wind stress curl) occurring offshore of the coastal boundary zone. A. Onshore Ekman transport and positive wind stress curl; convergence and downwelling at the coast, devergence and upwelling offshore. B. Onshore Ekman transport and negative wind stress curl; convergence and downwelling at the coast, continued convergence offshore. C. Offshore Ekman transport and positive wind stress curl; divergence and upwelling at the coast, continued divergence offshore. D. Offshore Ekman transport and negative wind stress curl; divergence and upwelling at the coast, convergence offshore.

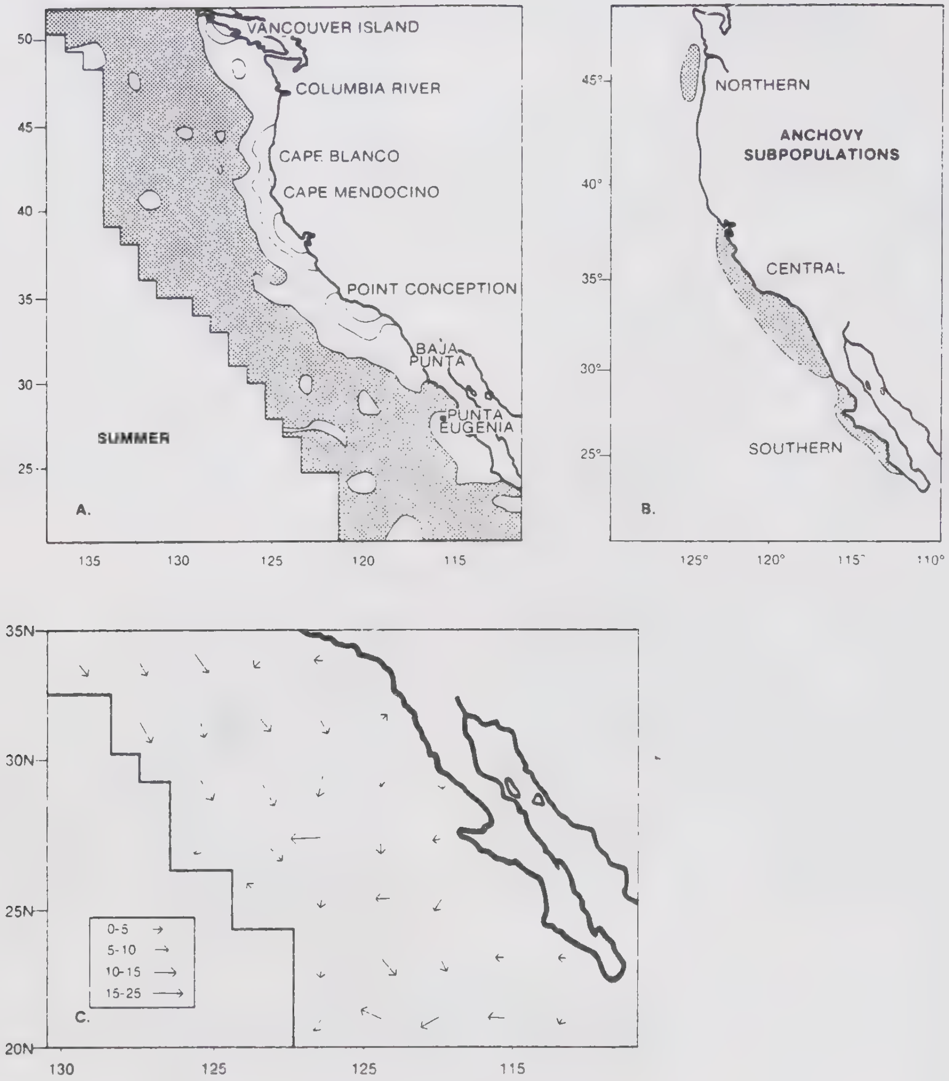
The smaller scale features of the stress and stress curl (Fig. 4(a)) distribution produced by Nelson (1977) by compositing many years of data, cannot be resolved by the observations generally available in a synoptic sampling (Fig. 1). Thus time series indicators can only be produced on a considerably larger scale (Bakun and Nelson, 1977). Estimates of fluctuations of wind stress features of the size of the negative curl lobe must presently rely on an untested assumption that such features would fluctuate in phase with and in the same sense as the larger scale pattern in which they are embedded.

Satellite Measurements

Measurements from earth-orbiting satellites have been heralded as the answer to many of society's environmental monitoring data needs. Recently, the U.S. Government placed into orbit a satellite (SEASAT-A) specifically designed for ocean science purposes. Satellite measurements have been valuable in indicating sea temperature structures as a tactical aid to fishing operations; satellites have also improved the weather advisory services which are vital to the operation of a fishery. However, we are not aware of their use to date on the fishery management problem.

The infra-red or microwave radiation sensors are not as yet accurate enough to define the subtle long-term variations which would be reflected in fish stock fluctuations. Satellite mounted altimeters may be capable of recognizing the existence of sea surface slopes characteristic of swift ocean currents such as the Gulf Stream; their precision does not yet approach that required to indicate fluctuations in broad-scale mean flow velocity in eastern boundary currents, although it may be adequate to recognize major eddy structures.

The wind sensing capabilities of satellites offer some very enticing prospects for uses in fishery management studies. The 50-km resolution which is designed for the microwave scatterometer which was placed on SEASAT-A would allow synoptic viewing of features the size of the negative wind stress curl lobe off central Baja California (Fig. 4(a)), i.e., on the scale that wind stress features may actually affect fish stocks.


VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
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NORTHERN
ANCHOVY SUBPOPULATIONS
CENTRAL
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B.
45°
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125°
120°
115°
110°
35N
30N
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20N
0-5 →
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10-15 →
15-25 →
C.
130
125
125
115

Figure 4. (a) Wind stress curl distribution during summer (June through August long term means). Contour interval is 0.25 dynes cm^{-2} per 100 km. Negative curl values are shaded; positive curl values are unshaded (after Nelson, 1977). (b) Spawning distributions of the central and southern subpopulations of northern anchovy (Paul E. Smith, personal communication). (c) Ship drift during October, November, and December. The small arrows, indicating mean drifts, are scaled according to the key at the lower left. Large arrows suggest the inferred circulation pattern (after Nelson, 1977).

Another general requirement for wide application to fishery management is that a data source be available in long time series so that models based on it can be verified against observed fish stock variations. This necessitates some years lag between the introduction of new technology systems such as satellites and telemetering buoys, and their usefulness in this sense. This delay can be eliminated if the new available information can be used to "calibrate" existing time series. For example, if the ability to view small scale wind stress curl patterns would allow us to define their relationship to the large scale synoptic weather patterns which can be defined by the density of synoptic ship reports available historically, models using the small-scale physical mechanisms could be based on the large scale time series.

Integrators of multiple processes

Where possible, it is preferable to use indicators of the particular processes which are actually affecting the organisms. Sometimes such indicators are either not available or else a precise notion of the relative importance of various processes may be lacking. In these cases, using time series which reflect more than one process or which are considered indicative of general environmental transitions may be the only resort.

An important example of this sort of time series is the Southern Oscillation Index (Bjerknes, 1969) which is indicative of major transitions in the coupled ocean-atmosphere system; Quinn (1978) has used this index to predict El Nino invasions off Peru. Indeed, El Nino itself has come to be regarded as an important index of Pacific-wide variations. Chelton (1980) has reported a correspondence between changes in the broad-scale background flow of the California Current and El Nino occurrence. Baumgarter, et. al. (1979) report that conditions in the Gulf of California are dominated by variations corresponding to El Nino occurrences.

Long time scale variations in atmospheric pressure are sometimes used as an explanatory variable in empirical studies of fish stock variation. (See section on Pacific mackerel, below.) It is unlikely that the actual pressure experienced by the organisms has any significant effect on survival; a change in depth of a couple of feet would involve pressure changes comparable to any atmospheric pressure fluctuations. However, just as barometric pressure is useful in indicating weather changes, it is related to variations in atmospheric effects on the ocean environment. Where low atmospheric pressure is related to occurrence of cyclonic storms, anomalous mean barometric pressure may be indicative of (1) anomalous Ekman transport conditions which disrupt upwelling normally produced at the eastern edge of a subtropical high pressure system, (2) negative wind stress curl, (3) increased wind-induced mixing of the upper ocean, (4) decreased solar radiation due to cloud cover, etc. However, each of these effects can be estimated separately; in our opinion it is preferable to indicate separately each process involved in as precise a manner as possible. If it is considered necessary, because of limited degrees of freedom, etc., to combine multiple processes into a single series this should be done in a rational manner, based on the available understanding of the interacting effects of the processes involved.

Other "integrators" which have been used in fishery studies include tree ring width (Cushing, 1979), sunspot activity (Favorite and Ingraham, 1978), and very long term average air temperature (Cushing, 1979).

Even carefully designed indices of individual processes can unavoidably become integrators of several interacting environmental effects. As described above, surface layer divergence indices indicate both the effects of the divergence or convergence of planktonic material and the linked effects of the wind stress curl on the geostrophic flow field. Upwelling indices are related to variations in upwelling or downwelling, offshore transport, and the near-coastal alongshore current. Sea temperature variations can be linked to biological variations through direct physiological effects, and through the dependence of temperature on upwelling, horizontal advection, and turbulent mixing. Obviously, the fishery-environmental problem is not simple, and in the situation of severely limited degrees of freedom, it is well to take great care to avoid generating statistical nonsense.

Independence of data points

Environmental time series are often found to contain a certain amount of serial correlation, i.e., a level of persistence affecting multiple data points. This can be caused both by real variations of period longer than the sampling interval and by inhomogeneties in the time series introduced by changes in sampling method, instrument location, etc. These causes are often difficult to separate.

For example, methods of producing atmospheric analyses such as are used as input data in Bakun's (1973) upwelling index computations have evolved from subjective hand analysis of reports in the 1940's and 1950's to fully automated objective procedures in recent years. In addition, the distribution of reports also changes over time; it is possible that the establishment of a reporting station in an area which was previously undersampled could cause a major disruption of the consistency of the indicator series. Even a direct measurement such as sea level is subject to vertical movements of the earth's crust upon which the gauge is mounted. Temperature series can be disrupted by such things as harbor construction near a measurement site, or by changes in the measurement technique such as the progressive conversion from bucket thermometers to sea water intake thermometers on reporting vessels.

Even when longer term features in a time series represent real environmental changes, they may be undesirable in an analysis. If a correlation is controlled by longer period features, the number of degrees of freedom assumed in order to estimate statistical confidence must be reduced to some fraction of the available number of data points. This represents a further limitation of the severely limited degrees of freedom typically available in fishery data series.

High-pass filtering of data series before testing for a relationship is one way to minimize the likelihood of arriving at unwarranted conclusions. If an apparent correlation disappears after high-pass filtering, then inhomogeneities must be considered as a source of error. The assumed degrees of freedom should be reduced to the number of observations which can be assumed to be independent of one another. (See section on Pacific mackerel, for example.)

POPULATION BIOLOGY CONSIDERATIONS

Population fluctuations of fishes are caused by an interplay between the biology of the organisms, (i.e. the genetic and age structure of the population) and the environmental conditions encountered by the population. In exploited stocks there is the further complication of alterations in the genetic and age structure of the population caused by selective fishing mortality. Before the understanding of a fisheries resource can go beyond rudimentary levels the stock structure of the resource must be adequately described. Knowledge of the number of reproductively isolated stocks, a description of their spawning grounds, distribution, and relative population size is a prerequisite to understanding their population dynamics. The lack of speciation in the pelagic fishes within the various eastern boundary current regions suggests that there is some degree of interchange within each region. In the pelagic fishes of the California Current region the number of reproductively-isolated stocks appears to be relatively small and these stocks appear to be separated into subregions which can be described by surface transport patterns (Parrish et al, Ms). Existence of smaller, reproductively-isolated units (stocklets) within the subregions has not been documented; however little research has been done to test this possibility. Once the stock structure is defined the principal research and management concern centers around the determination of fishing strategy that will maximize and stabilize long-term yield from the stocks or stocks. In small pelagic fishes the principal factor that prevents maximization and stabilization of yield is the high degree of variability in stock size.

Spawner-Recruit relationships

One of the most pervasive questions of fisheries biology is the relationship between parent stock size and reproductive success (usually refered to as recruitment). Near extremes of views on this question were presented in Clark and Marr's (1955) classic paper on the California sardine fishery. Clark suggested that at low and moderate stock sizes recruitment was directly proportional to parental stock size and that at high stock sizes recruitment declined with increasing stock size. Marr suggested that over the expected range of stock size recruitment was unrelated to stock size. These two views are shown graphically in Figure 5a. The relationship between parental stock size and reproductive success can be expressed in different ways. For example, is recruitment dependent upon parental stock size or is the rate of recruitment dependent upon stock size? In the first case the dependent variable is recruitment (i.e. numbers of recruits or recruit biomass) in the second case the dependent variable is the recruitment rate; (i.e. recruits per spawner or recruit biomass per spawning biomass). When viewed from the rate

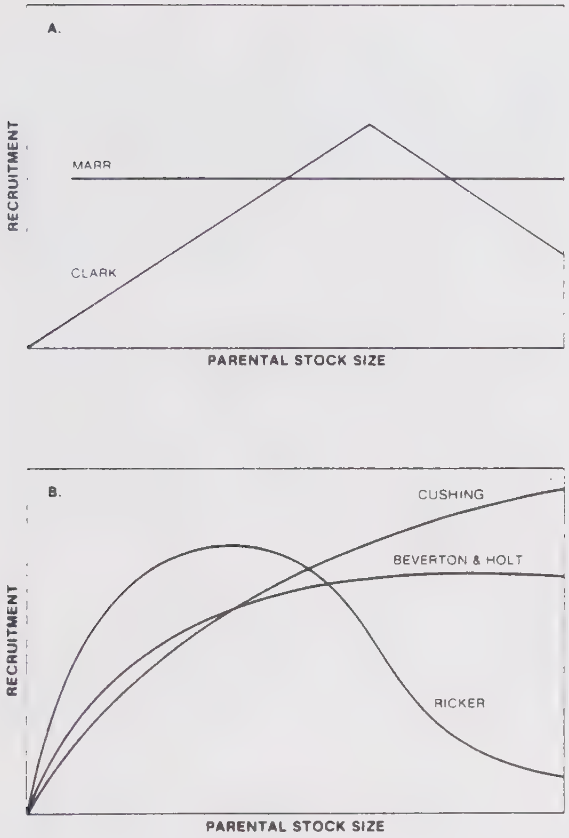

Figure 5. Stock-recruitment functions.

viewpoint Clark's model implies that recruits per spawner are independent of stock size at low and moderate parental stock sizes and are inversly dependent on parental stock size at high parental stock sizes. Marr's model implies that the number of recruits per spawner continuously declines as parental stock size increases; it is therefore density-dependent.

The recruitment rate can be viewed as the summation of a stock's reproductive, growth, and mortality rates up to the age at recruitment. If decreased stock size results in increased growth or reproductive rate or in decreased mortality, the recruitment is termed compensatory density-dependent. That is, the relative recruitment success increases at lower stock sizes. The mechanisms for this type of change include features such as intraspecific competition for food, lower growth rates, lower fecundity, and cannibalism at higher stock sizes. If the rate of recruitment decreases at low stock sizes the stock is said to have depensatory density-dependence. The principal mechanism suggested for depensatory density-dependence is increased natural mortality associated with smaller school sizes that might occur at small stock sizes (Clark, 1974).

The mathematics that have been used to describe the relationships between parental stock size and recruitment principally consist of alternative extinction curves. These extinction curves are used to describe the relationship between recruits per spawner and spawning stock size. The most commonly used models are those proposed by Ricker (1975: 282), Cushing (1971), and Beverton and Holt (1957: 49). These models are listed in Table 2 and shown graphically in Figure 5b. All three models have a density-independent term which can be envisioned as describing the intrinsic rate of increase, and a density-dependent term which is a compensatory term that has the effect of reducing the rate of increase as the stock size increases.

The Ricker (logistic) model has the largest compensatory term and implies that at high stock sizes recruitment is low; the potential shape of the Ricker curve is quite variable. The Beverton and Holt (asymptotic) model implies that at high stock sizes recruitment reaches an asymptotic maximum. The Cushing (allometric) model implies that recruitment increases with stock size but at a continuously decreasing rate.

TABLE 2. Stock-recruit models

Ricker: $R = a\ Pe^{-bP}$

Beverton & Holt: $R = P/(a + bP)$

Cushing: $R = aP^{-b}$

R = Recruitment
P = Parent stock size
a = density-independent coefficient
b = density-dependent coefficient

The choice of which model to use for a particular stock should be related to the hypothesis that is envisioned to limit the stock. If there is good reason to believe that there are very strong density-dependent effects in recruitment, i.e. if the spawning grounds are much more limited in size that the feeding grounds or if cannibalism by adults is significant, the Ricker model may be appropriate. The anadromous stocks of salmonids for which the model was originally developed are a good example for the use of the Ricker model. If the "gate mechanism" is expected, i.e. if nursing grounds have a relatively constant carrying capacity, the Beverton and Holt model is appropriate. The plaice (Pleuronedes platessa), for which the model was originally developed are a good example for its use. If the critical stage (or match-mismatch) hypotheses is considered to be the principal factor controlling recruitment the Cushing model may be most appropriate. The California stock of sardine is a good example for the use of this model (MacCall, 1979).

The Ricker model, due to its flexibility of shape, can approximate the shape of all three of the above examples as long as it is only applied to the stock sizes for which there is sufficient data to justify its usage. Of course none of the regression fits should be extended beyond the range of the data to which it was fitted. The methods used for fitting the various models include linear regression, linear regression with transformed variables, and iterative nonlinear regression. Models fitted with logrithmically transformed variables are fitted to the geometric mean rather than the arithmetic mean and are biased towards low expected values. Corrections for this type of bias are described by Beauchamp and Ohlson (1973).

Life History Stages

Stock-recruitment models work best if the observed variation from the model is small and random. The models give biased predictions if the variation from the model is large, if it contains time series trends, or if there is autocorrelation in the residuals (Sissenwine, 1977). The predictive capability of stock-recruitment models has not proven to be of great value in stocks of small pelagic fishes which have high natural mortality rates. This type of stock, in which recruits comprise a large proportion of the exploitable biomass, appear to be susceptible to recruitment overfishing during unfavorable environmental periods (Paulik, 1971; Cushing, 1975; Murphy, 1972).

Research into stock-recruitment relationships requires extensive age composition sampling of the catch and many years of data at different stock sizes. Recruitment, while not easy to measure, can be reasonably estimated in stocks which have large fisheries and extensive sampling of the catch. The fact that only one data point is accrued per year puts a severe limitation upon the determination of factors influencing recruitment processes. Stocks which have extended spawning seasons with potential multiple peaks, such as the Engraulis stocks of the Peru and California Current regions, have special problems in estimation of recruitment. In the California Current only two pelagic stocks have enough data at different stock sizes to produce statistically meaningful stock-recruitment relationships (The California stock of Sardinops (Murphy, 1966; MacCall, 1979) and the California stock of Scomber (Parrish and MacCall, 1978)). In both of these stocks the stock-recruitment relationships are characterized by very flat curves with a large amount of scatter in the data points. In both, compensatory density-dependent processes appear to be minor and the Cushing model, which implies that highest recruitment occurs at large stock size, provided the best statistical fit. However, over the range of stock size that is likely to occur with heavy exploitation the Cushing, Ricker, and Beverton and Holt stock-recruitment functions would all produce similar curves.

If a significant portion of the variation in recruitment is associated with environmental fluctuations, spawner-recruit models can potentially be improved by inclusion of the associated environmental terms. Recruitment is therefore probably best described with models developed with multiple regression. The Cushing and particularly the Ricker models have several features that make them the best candidates for the development of density and environmental-dependent multiple regression models. As Ricker (1975) has pointed out the effect of environmental variation is expected to be multiplicative. The dependent variable in these two models are logarithmically transformed variables which allows the environmental terms to be exponential terms which have geometric effects. The Ricker model is particularly well suited for the development of regression models as the dependent variable is the natural logarithm of recruits per spawner, or recruit biomass per spawning biomass (ln R/P). Therefore the terms which best describe the survival rate are those included in the model. If the model that best describes "ln R/P" is developed with stepwise multiple regression with parental stock size and environmental variables as independent variables the model will be less biased than the case where the environmental variables are regressed against the residuals of the Ricker model (i.e., if the residuals are the dependent variable).

The final multiple regression model, incorporating both density and environmental terms, can then be transformed (by exponentiation) to an expression of absolute recruitment. If desirable the bias in expected value resulting from the fact that the model is fitted to the geometric mean of the observed data can then be avoided by nonlinear regression. The coefficients developed with the stepwise multiple regression can be used as starting values in an iterative nonlinear regression. Environmentally-related variation is likely to be the result of many biotic and abiotic processes. Due to the limited number of observations and attendant problems with degrees of freedom only a small number of terms can be statistically justified. Therefore unless the environmentally-related variations in the rate of recruitment are dominated by one or a small number of environmental processes or features the inclusion of environmental effects is unlikely to be of much benefit.

The processes regulating the populations of exploitable marine fishes break naturally into three stages, based both upon life history phases and data sources. These stages are the early life history, juvenile and post-recruit stages. The early life history stage is limited to the period when the organisms are largely planktonic. This stage is characterized by very high mortality. The bulk of information concerning this stage comes from egg and larval surveys, field studies and laboratory experiments. The early life history, as used here, ends at about the time that the larvae become mobile enough to avoid egg and larvae survey nets. The juvenile stage is essentially the stage that is unsusceptible to capture by either egg and larvae survey nets or commercial fishing gear. From a modelling viewpoint the feature that characterizes this stage is the lack of information. The post-recruit stage is the stage that is susceptible to capture by commercial gear. A large proportion of the knowledge of this stage consists of information gathered from the fishery.

Modelling of any one of these three life history stages is a difficult task and there presently are no stocks for which fully developed models of all three life history stages are developed. Modelling of the individual life history stages is dominated by models of the post-recruit stage with a lesser total effort on the early life history stage and practically no effort on the juvenile stage. Modelling of any one of the life history stages must necessarily ignore many of the relationships and processes that occur in the other life history stages. The following sections describe some of the weaknesses of models which concentrate on only one of the life history stages.

Post-recruit modelling

The bulk of the current population models of fish stocks is composed of models which are focused on the post-recruit stage. Adequacy of the models is primarily limited by first order approximations of the parameters which describe the growth, mortality, and recruitment rates. Population fluctuations occur through the alteration of one or more of these rates and the mechanisms that cause these alterations are largely related to differences in stock size, environmental conditions and age composition of the stock. Determination of relationships of the environmental state, stock age composition and stock size to growth, mortality and recruitment rates requires data from extensive long-term sampling programs. Such data are very sparse and most of our current information is from a few well-studied stocks.

Growth is the easiest of the three required rates to measure. In addition, large numbers of samples can be taken each year. Growth, therefore, is the best described rate. For purposes of describing age-dependent growth, samples are largely independent if taken through catch sampling programs or exploratory fishing. This independence does not extend to the testing of the relationship between stock size and growth rate or that between environmental state and growth rate. For the testing of these relationships only one observation accrues per year and these observations may be autocorrelated.

Documentation of changes in growth associated with changes in stock size of post-recruit fishes is not common in the literature (Murphy, 1977). This may be partially due to the fact that data is not often collected in a manner to show such changes. For example, weight at age is a more meaningful measure of growth than the more commonly used length at age. Of course a stock must also fluctuate over a wide range of stock size before a relationship between stock size and growth rate can be determined. Another reason that density-dependent changes in the growth rate are uncommon or relatively small is that when surplus energy is available it may be utilized for gonadal growth rather than somatic growth. Compensatory gonadal growth can occur through earlier age at maturity, increased batch fecundity or increased numbers of spawnings per year. Earlier age at maturity at lower stock size is a common feature in the stocks of small pelagic fishes of eastern boudary currents and has been described in the California stocks of sardine (Murphy, 1966) and mackerel (Parrish and MacCall, 1978) and the Peru stock of anchoveta (Valdivia, 1978). Verification of variation in batch fecundity or number of spawnings per year is presently unavailable and will be difficult to obtain. Fecundity is usually considered to be proportional to body weight and is often expressed as the number of eggs per unit body weight. If this is the case, even if there are no compensatory changes in the number of eggs per unit weight, fecundity will increase with compensatory changes in the condition factor such as described for the California stock of sardine (MacGregor, 1959). Availability of surplus energy can be the result of compensatory density-dependence or favorable environmental state; with a limited set of observations it is difficult to sort out the two factors. Mortality rates are very difficult to measure accurately and natural mortality in exploited stocks is confounded with fishing mortality. Essentially nothing is known of the dependence of mortality, in the post-recruit stage, upon stock size or environmental state. Heavily exploited stocks of small pelagic fishes often exhibit increased total mortality with increased age within the post-recruit stage (Paulik 1970). It is not known if this is due to increasing natural or fishing mortality.

Modelling juvenile fishes

The present information on the juvenile stages of the pelagic fishes of eastern boundary current regions is too incomplete to be of much use in population modelling. Information on mortality rates and on the processes affecting mortality is lacking. The available field data base is largely limited to general descriptions of geographical distribution plus some information on sizes of fish. Data is needed on the vertical distribution of juvenile fish. Laboratory data is largely limited to growth data which is not verified against field data; although with the new daily aging techniques (Methot and Kramer, 1979) this is an area of active research.

The stock-recruitment relationships discussed previously group the processes affecting the early life history and juvenile stages into a single process (i.e., recruitment). The relative effect of the early life history and juvenile stages in determining recruitment fluctuations is not known. And it obviously must be determined separately for each stock. Although the early life history stage is critical on the short time scale, in that it has very high mortality, there is little evidence that year class size can be predicted by the numbers or concentrations of large larvae. For example, Smith (1978) has shown that the ratio of large larvae was nearly constant over the period of 1952 - 1956 and has suggested that the largest source of variation in sardine year-class size occurred during the juvenile stage. One of the most perplexing problems concerning recruitment processes in upwelling areas is the contribution of the large concentration of larvae which are found well offshore of the slope.

Modelling the early life history stage

Modelling of the early life history stage involves problems comparable to those of the post-recruit stage in addition to those particular to the early life history stage. The value of post-recruit models is largely determined by how well they predict the potential yields to the fishery and their adequacy is very sensitive to the accuracy of their stock-recruitment functions. Early life history models will eventually be evaluated on how accurately they predict the number of larvae entering the juvenile stage. The adequacy of early life history models will in a similar way be sensitive to the accuracy of stock-egg functions.

Both juveniles and post-recruits have the potential to reduce the survival of eggs and/or larvae through cannibalism or competition for forage. They also have the potential to increase the survival of eggs and larvae through predation on potential egg and larval predators. However, the most obvious effects that the post-recruit stage has on the early life history stage are those associated with the production and spawning of eggs. The numbers of eggs, their quality, and their distribution in time and space are determined by processes affecting the post-recruit segment of the stock. Fecundity and egg quality can be altered by density-dependent or environmentally related variations in the growth rate, condition factor, age at maturity, number of spawnings per year, and age structure of the post-recruit segment of the stock.

The distribution of eggs in time and space is influenced by oceanographic conditions (i.e. temperature, currents, food availability, wind events) which affect the geographical distribution of the adults. Features which trigger spawning, although not well understood, could also include oceanographic conditions. Stock size also alters the geographical distribution of spawning as a stock may increase the size range, of its spawning grounds as stock size increases. The stock may also saturate the available spawning grounds in both time and space when the stock is large. If this occurs the variance in the stock recruitment relationship should increase as stock size decreases. The age structure of the stock influences the time of spawning as older fish often start spawning earlier in the season than first time spawners. With species that have multiple spawning, older fish may have a longer spawning season than first-time spawners.

The rates at which all of the above relationships between adults and their eggs and larvae occur are potentially density-dependent. Density-dependent rate increases are more likely when lowered population size is caused by exploitation rather than when it is caused by environmental changes which may independently affect the rates at which the processes occur.

Several extremely sophisticated larval fish models have recently been published. (Vlymen, 1977; Beyer, In press) These models are well designed to model individual spawning spots. Thus they are in many ways analogous to yield-per-recruit models in that they describe the survival and growth of a given amount of eggs or larvae. For the purposes of predicting reproductive success or recruitment of individual stocks for management purposes these types of models have severe limitations. The models were, of course, not intended for management purposes. The results of these models are dependent upon given environmental states. The limitations of the models are not primarily due to the structure of the models but rather to the lack of knowledge of the environmental variables in the models. Determination of the average environmental conditions encountered by eggs and larvae in a given year is beyond our present capabilities and resources. Even if we were able to establish the mean environmental conditions encountered by eggs and larvae it is likely that the use of mean data would not result in good predictive capability due to patchiness problems. The survival of individual eggs and larvae is dependent upon interactions that occur on very small space and time scales. These interactions are associated with processes which operate on a wide range of scales. Thus the survival from individual spawning spots is affected by a range of space scales from that of less than the size of a spawning spot to that of at least the size of the spawning grounds and a range of time scale from less than hours to at least the length of the spawning season plus the length of the early life history stage.

A possible solution to the integrating problem is the use of spatial compartment models to account for environmental state patchiness in the larger space scales. Smaller-scale patchiness could be accounted for by stochastic terms. Unfortunately while the environmental state may be considered to be an additive process the response of individual spawning spots to environmental conditions is not additive. For example the survival of larvae after two days of starvation is dependent both on the age of the larvae and the feeding conditions, (i.e., environmental state) on the days preceding the two days of starvation. The spatial compartment model must therefore include age groups. The fact that processes affecting egg and larvael survival operate on short time scales implies that the models must be run with short time steps. Thus, the combination of requirements for adequate spatial detail, age composition, and short time steps will result in the requirement of a huge computer and considerable running time.

An alternative to the use of a large compartment model, which also requires less conceptual alteration of existing larval models, is to model individual spawning spots. The models could be moved around in fields of the environmental state as Lagrangian drifters.

Eastern boundary current pelagic fishes have such extensive spawning grounds and extended spawning seasons that integration of scales becomes a major, perhaps dominant feature of any predictive model of the early life history stage.

RECENT ADVANCES - CALIFORNIA CURRENT REGION

Anchovy

The data base on the northern anchovy Engraulis mordax is different from those for the other better known species in the California Current Region in that the majority of information comes from field and laboratory studies rather than being taken from the fishery. There is more information available on eggs and larvae than on post-recruits. Most recent larvae work is well discussed in companion papers in this volume; we will therefore limit our discussion of recent anchovy research generally to processes having a larger scale than that affecting individual larvae.

The anchovy is widely distributed throughout the California Current System. Blood serum studies (Vrooman and Smith, 1971) show that there are three reproductively-isolated stocks (Fig. 4(c)) which exhibit considerable differences in their seasonality of spawning. The spawning grounds of the stocks appear to be separated by oceanographic features. The northern and central stocks are separated at the Northern California upwelling maximum (Parrish et.al., MS) and the central and southern stocks are separated in the region where negative wind stress curl approaches the central Baja California coast (Fig. 4(b)). The bulk of the information available on the anchovy concerns the central stock which extends from about 29° N to 38° N.

The central stock of the northern anchovy, like the anchoveta of the Peru Current, spawns to some degree all year round, with peaks in February-March and August-September. In both the peak in the winter-spring transition is greater than the peak in the summer-fall transition.

Lasker and coworkers (Lasker 1975, 1978; Lasker and Smith, 1977; Lasker and Zweifel 1978; Smith and Lasker, 1978) have shown that first feeding is a critical period for anchovy. Success of first feeding is associated with the occurrence of small scale concentrations of dinoflagellates which can be dispersed by wind events. However, the fact that the anchovy has such a long spawning season makes it very difficult to predict recuitment on the basis of indices of wind stress or other environmental data. Good environmental conditions during any part of the year could conceivably dominate annual recruitment. A recent breakthrough on daily aging (Methot and Kramer, 1979) greatly enlarges the possibilities for analysis of the relationships between environmental conditions and larval survival. Adequate sampling of pre-recruits coupled with daily aging will allow assessment of the time of year and associated environmental conditions which result in significant recruitment.

MacCall (1979) has noted a correspondence between low second quarter (April-June) values of the upwelling index (Bakun, 1973) at 33° N in the period 1947 to 1952, and extremely low anchovy biomasses in the early 1950's. This corresponded to apparent recruitment failures in sardine in 1949-50 and Pacific mackerel in 1949-50-51 and to disappearance of bonito (Sarda chiliensis) in the late 1940's and their reappearance in 1954.

We might add that upwelling index values at 39N, which characterize the Cape Mendocino - Point Arena area where the most vigorous upwelling in the California Current system occurs, were chronically low through the second half of the 1940's. This may have adversely affected the general level of productivity throughout the entire system (See sardine model, below.) Thus the low spring upwelling of 1947-52 local to the Southern California Bight may have been superimposed upon poor conditions which were advected from the upstream upwelling maximum.

Two recent studies indicate direct interactions between adult and larval processes. Hunter and Goldberg's (1980) work on batch fecundity shows that the northern anchovy spawns approximately once a week over an extended spawning season, indicating that energy reserves and the availability of food to the anchovy may influence the number of spawnings per year. Hence total fecundity may be a function both of adult anchovy biomass and food availability. Hunter and Kimbrel (in press) found that approximately 17 percent of eggs spawned were cannibalised by filter-feeding anchovies, and they estimate that this may represent about 32% of the natural mortality of anchovy eggs.

Pacific mackerel

Substantial catches of Pacific mackerel commenced off California in the late 1920's. Economic conditions at the beginning of the 1930's caused a large drop in fishing effort, but a recovery of prices and demand resulted in rapid expansion of the fishery from 1932 to 1935. Landings reached a peak of 66,500 MT in the 1935-36 season. Thereafter, the fishery went through a long, fluctuating decline. In the 1953-54 season the fishery was nearly exhausted, but good recruitment in the 1950's (Fig. 6) rejuvenated the fishery for a while until a series of poor recruitments in the 1960's brought it to a temporary close. Recently the population has rebounded strongly.

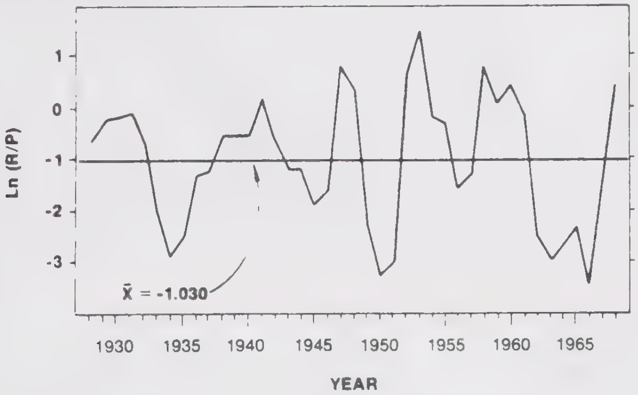

Figure 6, Time series of the natural log of the observed recruit biomass per spawning biomass in the California Current stock of Pacific mackerel, Scomber Japonicus.

A detailed analysis of the fishery, including population biology, cohort analysis, spawner-recruit models, and yield simulations, was presented by Parrish and MacCall (1978). Here we briefly abstract certain of their main findings concerning environmental dependence. These are in the area of empirical environmentally-dependent spawner-recruit models. Their post-recruit models do not address any environmental dependence, incorporating the usual assumptions of constant natural mortality rate, etc.

The authors consider a number of environmental variables, which are assumed to act mainly during the May-July spawning period. Thus, they are hypothesizing that environmental effects on Pacific mackerel recruitment occur at the spawner-egg and the early life history phases. Several linear combinations of months were considered, including (1) a simple average over the 3-month May-July period of peak spawning, (2) a simple 3-month April-June average to test for lagged effects (e.g. upwelling would provide suitable food particles only after some lag, assumed to be of the order of one month), and (3) "prorated" averages of both 3-month periods, where each monthly contribution is weighted by an estimate of the percentage of spawning which occurred during that month in each particular year of the time series.

The environmental variables for which these linear combinations produced the best correlations with recruitment are given in Table 3 (Parrish and MacCall's Table 18). Other variables tested which did not yield significant correlations included Saur's (1972) index of very large-scale subtropical gyral circulation based on Hawaii to San Francisco sea level difference. Separate tests against all the individual monthly values produced lower correlations than those against the linear combinations (Table 3) considered characteristic of the entire spawning season.

TABLE 3. Correlation Coefficients of Linear Combinations of Monthly Values of Environmental Variables with logarith of Pacific mackerel recruitment.

Variable	N	May-July mean	Prorated May-July	April-June mean	Prorated April-June
SPIER	41	.270	.416**	.276	.255
BARP	41	.030	-.165	-.007	-.059
SSTC	38	.434**	.432**	.432*	.392*
WINDC	38	-.354*	-.380*	-.289	-.306
SLLJ	41	-.542**	-.391**	-.514**	-.392**
SLEV	41	-.509**	-.348*	-.509**	-.366*
UP	23	.458**	.319	.575**	.713**
CURL	23	.528**	.610**	.486*	.584**

SPIER -Sea surface temperature at La Jolla
BARP -Barometric pressure at San Diego
SSTC -Sea surface temperature, Marsden Square quadrant 120(2)
WINDC - Wind speed, Marsden Square quadrant 120(2)
SLLJ -Uncorrected sea level height at La Jolla
SLEV -Sea level height at La Jolla corrected for atmospheric pressure
UP -Upwelling index at 30°N
CURL -Wind stress curl (surface layer divergence) index at 30°N
* -Significant at 5% level
** -Significant at the 1% level

The highest correlation of all was found with the April-June composite upwelling index, which is conceptually satisfying since upwelling would be expected to have a lagged effect. Highest correlations with sea temperature and with surface layer divergence (wind stress curl) were with the May-July prorated variables, again conceptually satisfying since these effects would seem to act directly on the larvae without lag. The correlation coefficients with temperature are positive, suggesting that warm temperature contributes to reproductive success; in this case the temperature appears to indicate a physiological effect, since a temperature-upwelling-productivity linkage would result in negative correlation coefficients with temperature. The correlations with surface divergence were positive; this is somewhat puzzling since one would expect convergence (negative divergence), by concentrating food organisms, to favor survival. Perhaps convergence could be detrimental by concentrating mackerel larvae in frontal structures where they would be highly vulnerable to predation. An alternative explanation could be that the relaxation of the blocking of northward coastal counterflow by the negative wind stress curl lobe off central Baja California could have allowed augmentation of the exploited northern subpopulation by the southern subpopulation (See subsection on convergence-divergence in the section on environmental variability, above). Negative correlations are found with coastal sea level; this could be related to the upwelling effect since strong upwelling would tend to depress coastal sea level.

Parrish and MacCall present a number of empirical models containing various formulations of density-dependence (including those presented in Table 1 and in Figure 5(b)) and the environmental variables (Table 3). Since the upwelling index and surface divergence index series are available only since 1946, models containing these variables treat only the latter part of the historical record of the fishery. In order to retain reasonable degrees of freedom for each explanatory factor these models were restricted to a density factor and two environmental factors. Models treating the total time series were allowed to contain three environmental factors in addition to a density dependent factor. None of the density dependent formulations were as significantly correlated with recruitment as were various environmental terms; density dependence alone could account for no more than 24% of the observed variation. However, the authors felt that some form of density dependence was a conceptual necessity and so a density dependent formulation was forced to appear in each multiple regression model. However, the fitting of the density dependence was accomplished in concert with the environmental terms. This is a fundamentally different procedure than that used by Nelson, Ingham and Schaff (1977) who first fitted an assumed density dependence and then fitted environmental variables to the residuals. In our opinion the procedure of Parrish and MacCall is more valid, since fitting a density dependence before accounting for environmental variation assumes that environmental variability does not affect the fit; if this were the case there would be little need to include environmental terms.

A model containing a Ricker density dependence, and an upwelling index and a wind stress curl (surface layer divergence) index as environmental terms, was significant at much greater than the 99% level and explained 76% of the observed recruitment variation since 1946. A model containing sea temperature, coastal sea level and barometric pressure, as well as a Ricker function was again significant at the 99% level and explained 59% of the variation in the longer series covering the total fishery.

The two intense declines in the Pacific mackerel stock correspond to periods of poor recruitment in the late 1940's and early 1950's and in the mid, 1960's (Fig. 6). During the first period, there was an extended series of poor upwelling years in the upwelling maximum region off Northern California (Bakun, 1973). During the decline in the 1960's, anomalously low upwelling in the local Baja California spawning area was indicated. It is interesting to note that in the recent period, not treated by Parrish and MacCall, extremely vigorous upwelling is indicated for the mid 1970's, while excellent relative reproductive success in 1974 and 1976 has enabled the Pacific mackerel stock to rebound from its previous collapsed state.

The environmentally-dependent functions produced by Parrish and MacCall have allowed them to run simulations of management options containing a realistic spectrum of environmental variance, i.e. an aperiodic cyclic pattern as opposed to the random environmental noise usually assumed (e.g. Allen 1973, Walters, 1975). These simulations have been used by the State of California in establishing a management strategy for Pacific mackerel, which is now in operation.

Before concluding our survey of this work, a comment on independence of data points is relevant to the purpose of our present paper. The ratio of recruitment to parental biomass (Fig. 6) obviously contains substantial autocorrelation; the series in no way resembles random "white" noise. Rather, runs of multiple years of good and poor recruitment dominate. In this case the assumption of an independent data point each year probably results in a substantial overestimate of available degrees of freedom (Table 2). However, one can visually convince himself that there are at absolute minimum some ten or eleven independent data points determining the function in Fig. 6 and at least eight in the series since 1949 (by counting extrema or crossings of the zero line, etc.). A recomputation indicates that the significance of Parrish and MacCall's major relationships is still at an acceptable level even when the assumed degrees of freedom are so reduced. However, in cases where the relationships may be less pronounced, this issue of independence of data points may be critical. A formula for choosing the reduction in degrees of freedom in an autocorrelated time series is presented by Sutcliffe, Loucks, and Drinkwater, (1976).

Sardine

The Pacific sardine (Sardinops caerulea) fishery expanded rapidly in the years prior to World War II to become the largest fishery in the United States with 774,000 MT landed in the 1936-37 season. The exploited stock spawned in the region of stability and favorable transport south of Point Conception (Parrish, et. al., MS) but during the period of abundance migrated as adults to feed in the region of vigorous upwelling to the north, an important fishery arising as far north as Vancouver Island. A period of relative stability in the catch ended in 1945, whereupon the catches begin to decline disastrously to the point where the fishery essentially vanished in the early 1960's.

There are two sets of recruitment estimates published for this stock. Murphy's (1966) cohort analysis presented numerical values through 1960. In this analysis, Murphy assumed a change in natural mortality rate from 0.4 in the years previous to 1949, to 0.8 in subsequent years in order to match independent stock estimates based on egg and larvae surveys. MacCall (1979) showed that this change was unnecessary and presented recruitment estimates through 1965.

Since no studies of sardine which incorporate time series indices of environmental processes have yet been published, we here present results of a preliminary hypothetical model formulated to include density dependence and environmental effects represented by upwelling index and wind stress curl index time series. Four such time series were hypothesized as indicative of environmental effects on larval survival.

These included an upwelling index and a wind stress curl index computed at 30° N latitude (symbols: UP30 and CURL30), found by Parrish and MacCall (1978) to be the most significant variables in their Pacific mackerel model, and a wind stress curl index at 33° N latitude (CURL33), considered characteristic of surface layer divergence within the Southern California Bight and possibly related to the strength of the gyral circulation in that area. Each of these three index series was averaged over the 5-month period, February through June, of maximum sardine spawning (Murphy 1966).

A fourth environmental variable (UP39) is the average over the calendar year preceding spawning of the upwelling index computed at 39° N latitude. The inclusion of this variable, which does not characterize the specific season or the location of spawning, was motivated by correlations noted between longer-term upwelling index variations (Fig. 7) in the area of the Northern California upwelling maximum and indices of spring zooplankton abundance[5] in the downstream areas extending from Central California to southern Baja California. A multivariate response such that strong upwelling off northern California during the previous summer and fall quarters was associated with highest zooplankton concentrations in the downstream offshore regions relative to the concentrations directly inshore of those regions was the most robust relationship found. The spring zooplankton concentrations in the various offshore regions along the coast have a tendency to vary directly with the northern California upwelling index but the various univariate relationships are less pronounced than are those which are associated with the multivariate nearshore/offshore contrast (significance: .90 v.s. .98).

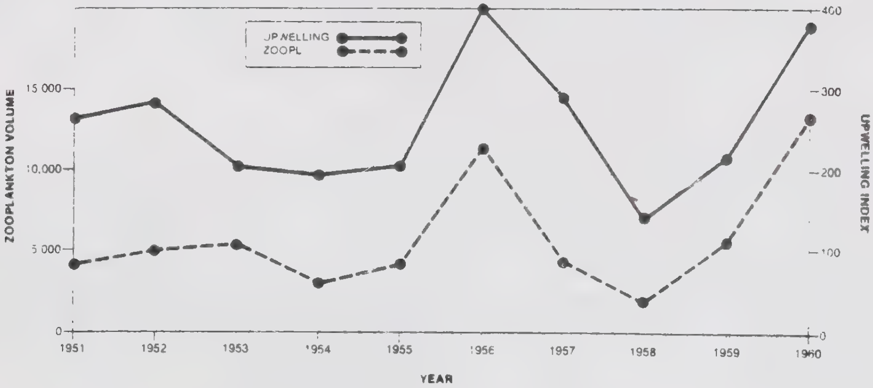

Figure 7. Central California offshore zooplankton abundance during spring (Paul E. Smith, personel communication v.s. upwelling index at 39N latitude (Bakun, 1973) averaged over previous 12 months.

Density dependent effects were incorporated by including parent stock size as a variable (STOCK). A final variable which was a simple linear trend (TREND) was added to reflect long-term changes, such as possible competition due to the rise of the northern anchovy population during the time period modeled. The modeled period covered only the decline of the stock since the upwelling and wind stress curl indices are not presently available for the period prior to 1946.

We expect the effects considered to alter the proportion surviving of whatever number of eggs were spawned rather than "killing" or "not killing" any fixed number. Since we wish as much weight given, for example, to a halving of expected recruitment as to a doubling, a regression against the logarithm of the ratio of recruits to spawners is appropriate. The formulation of our model is therefore:

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[5] Personal communication, Paul E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92037.

$$\mathrm{Ln(RECRUITS/STOCK)} = a_0 + a_1\mathrm{UP30} + a_2\mathrm{UP39} + a_3\mathrm{CURL30} + a_4\mathrm{CURL33} + a_5\mathrm{STOCK} + a_6\mathrm{TREND}$$

Note that upon transformation to a prediction equation by taking the exponential of this model equation, the term containing the variable STOCK corresponds to a Ricker function (see Table 2).

The model was run on both the Murphy and MacCall population estimates; we look for results which are consistent in the analysis of both of the two separate sets as being perhaps less subject to distortion by deficiencies in our knowledge of the real population variations.

Against MacCall's estimates the full model was significant at 0.95. When the two least significant variables, UP30 and CURL30, were dropped from the model the significance improved to better than 0.99 ($r^2 = .7$). Regression coefficients were positive for variables UP39 and UP30, and negative for CURL30, CURL33, STOCK and TREND. Thus strong upwelling appears to favor survival, strong curl (surface layer divergence which would oppose formation of concentrated patches or organisms) corresponds to decreased survival. There appears to be compensatory mortality (negative coefficient for STOCK) and an apparent declining trend in survival over the period (possible competition from the increasing northern anchovy population). Of course the regression coefficients for UP30 and CURL33 should not be taken very seriously since significance increased dramatically when these variables were dropped.

The most significant variable by itself is UP39; the regression against this variable alone is significant at above .90. However, with STOCK and TREND in the model with UP39, UP39 is the least important of the three in reducing unexplained variance. The model with STOCK and TREND only is significant at .995; however, against either STOCK or TREND alone the regression is completely non-significant. The model with the three variables STOCK, TREND and UP39 is significant at better than .995 ($r^2 = .67$).

Murphy's (1966) estimates yield a series five years shorter than MacCall's (Fig. 8). This further depletes the seriously limited degrees of freedom. In this case the full model has an R-square of 0.92 and is significant at the 95 percent level. UP39 and UP30 have positive regression coefficients, STOCK and TREND have negative coefficients, as before. CURL33 has a negative coefficient as before but now CURL30 has a positive coefficient. This positive effect of a lessening of the ordinarily negative values of CURL30 is the same pattern noted by Parrish and MacCall in (1978) for the Pacific mackerel. The most significant single variable is STOCK, yielding significance at better than 90 percent and an R-square of .30. If TREND is then added, significance increases to the 99 percent level. If UP39 is introduced at this point its added contribution is significant at the 95 percent level. Subsequent addition of CURL30 to the model already containing STOCK, TREND, and UP39 is significant at somewhat better than 90 percent. The model containing the four variables, STOCK, TREND, UP39, and CURL30 is significant at better than the 99.5 percent level. R-squared is .92.

The variable UP39, which is designed to measure the effect of annual-scale variations in the northern California upwelling maximum, has appeared as an important factor against both population data sets. A period of generally weak upwelling commencing after the Second World War lasted through 1963, (Bakun, 1973) broken only during 1951 and 1955-56, which as a matter of fact were followed the next year by relative sardine year-class success (Fig. 8) and 1959, when the population was already at quite low levels. Murphy (1966) has reported a tendency for the spawning of sardines, before the population collapse, to be situated offshore relative to the spawning of anchovies. We have here noted the tendency for UP39 to reflect increases in offshore zooplankton concentrations relative to those near the coast during the spring spawning season. It seems a possibility that the long term variations in upwelling in the upwelling core of the California Current region could have been a factor in the rise of the anchovy at the expense of the sardine.

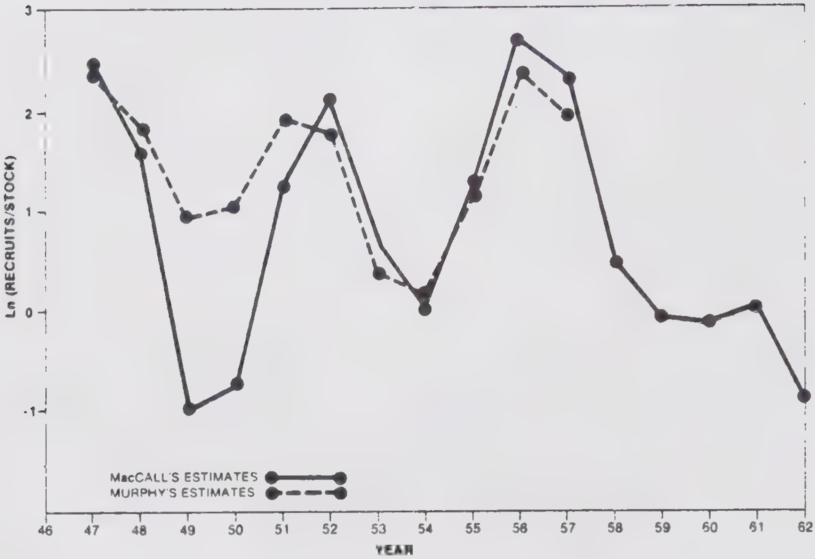

Figure 8. Natural log of the ratio of recruits (10^6 fish) to parental biomass (10^3 metric tons) based on the estimates of Murphy (1966) and MacCall (1979) over the modeled period of decline of the Pacific sardine fishery.

Regression analyses of both data sets indicate a compensatory effect of stock size and a negative trend in the rate of recruitment of sardine after 1946. The compensatory effect was obviously not strong enough to keep the population from collapsing under the combined effect of heavy exploitation and a declining trend in the rate of recruitment. The declining trend in the rate of recruitment could have been related to increasing competition with the rising anchovy population or it could be the result of overestimation of the potential spawning biomass due to an increasing proportion of sardines of southern origin as the stock declined as was suggested by MacCall (1979).

Again this is a situation where the data offer some tantalizing indications, but the available degrees of freedom in the historical time series are far too limited to yield final conclusions.

Hake

Substantial catches of Pacific hake (Merliccius productus) commenced abrubtly in the mid-1960's. Smith (1975) has reported a geographical shift in larval hake abundance, coincident with the heavy fishing pressure, such that larvae became more abundant off Central California and less abundant off Baja California. He hypothesized a linkage whereby the fishery resulted in a relative depletion of larger sized fish, which may either have traveled farther south to spawn or have participated in multiple spawning, the latter of which would have occurred farther south along the annual migration route.

Bailey (In press) presented a model supporting this hypothesis and further showed that the offshore extent of larvae off Central California was correlated (r = 0.70, significance 0.99) with offshore transport as indicated by interyear variation of the January monthly upwelling index (Bakun, 1973) at 36° N latitude. Off Baja California no such correlation was found. Bailey suggests that, since hake larvae tend to be distributed near the top of the thermocline, a deeper surface mixed layer off Baja California could perhaps protect the larvae from offshore transport.

Bailey (MS) constructed an index of yearclass strength from annual trawl surveys by summing the percentages of the total age composition contributed by each cohort over the ages 4-6 years. Over 14 years of available data, January offshore Ekman transport is negatively correlated (r = 0.73, significance 0.997) to this year class index; offshore transport during the winter spawning season appears to be detrimental to reproductive success, in agreement with the hypotheses presented by Parrish et al (MS). If larvae spawned off Baja California are indeed relatively protected from offshore transport, and the shift of spawning intensity to the less protected Central California region was indeed caused by the operation of the fishery, this situation presents an additional mechanism by which fishing pressure may adversely affect resilience to environmental perturbation.

Temperature does affect the situation. Bailey (In press) indicates more northward spawning in warm years relative to cold years. In addition egg and larval survival seems to be better in warm years judging from numbers of large larvae found in the spring. Bailey found that when a temperature index was added as a second explanatory variable to the regression of year class strength against Ekman transport, 69% of the variance in year class strength (r = 0.83, significance 0.998) is accounted for.

Bonito

The Pacific Bonito, Sarda chiliensis, has been fished commercially in the California Current region since the beginning of this century. Collins and MacCall (1977) have summarized the available information on the population dynamics and biology of the California Current stock.

Historically, the landings have fluctuated widely. The population appears to be centered near Sebastian Vizcaino Bay in central Baja California while much of the exploitation occurs off Southern California. The Southern California fishery apparently operates on two stock segments, one of which migrates annually northward from the population center and the other of which is a transient resident population which becomes established during periods of particulary favorable local conditions. Thus it is difficult to separate fluctuations in stock size from variations in availability to fishing operations.

Collins and MacCall constructed an index of relative recruitment success from estimates of spawning biomass derived from aerial surveys and estimates of recruitment based on catch per unit effort (CPUE) of the partyboat sport fishery (MacCall, Stauffer and Troadec, 1974). They found a positive relationship between this index and the upwelling indices (Bakun, 1973) off northern Baja California averaged over the March-July spawning season. Previous to 1963 no aerial surveys were available. For this period Collins and MacCall used the ratio of CPUE during a given year to the CPUE of the year previous to indicate relative recruitment success and to demonstrate a similar relationship to upwelling index as was found for the later period.

Dover sole

Many of the pleuronectids of the California current region have extended pelagic phases. Dover sole, Microstomus pacificus, which is the dominant commercial flatfish of the region, has larvae which are pelagic for up to a year; it is a late winter - early spring spawner. Off Oregon younger larvae are common both inshore, over the continental shelf, and offshore. Larger larvae are most common in waters outside of the continental shelf but during the winter there is an increase in the largest larvae over the shelf and slope where they settle (Pearcy, et. al., 1977). Hayman (1978) used fishery-based estimates of year-class size of Dover sole to determine the relationship between recruitment and oceanographic conditions. He found that recruitment was associated with reduced offshore Ekman transport during the period of maximum upwelling off Oregon (June-July) and with increased convergence during the Dover soles' settling period (December-January). It appears that increased offshore dispersal, during the period of the year when upwelling prevails off Oregon, is associated with reduced recruitment of the Dover sole and that wind-related features during the winter settling period also affects recruitment.

Rockfish

Little is known about the population fluctuations of rockfish in the California Current, but it seems useful to our discussion of drift responses to present some anecdotal information. In the California

Current region there are nearly 60 separate species of the genus Sebastes which are known by the collective term rockfish. The existence of such a variety of species in the very dispersive medium of an upwelling system may be facilitated by their livebearing mode of reproduction which produces young which may be capable of maintaining position relative to very specific ocean depths, bottom types and other conditions. Most of these species release young in the late winter when offshore surface transport is most relaxed (Parrish, et al., Ms). The larvae are pelagic for 4-6 months and the juveniles are observed to congregate in the inshore region in the summer. It is known that occasional good year-classes pass through the fishery; however, until very recently the fishery has not been regularly sampled and the relative sizes of individual year-classes is unknown.

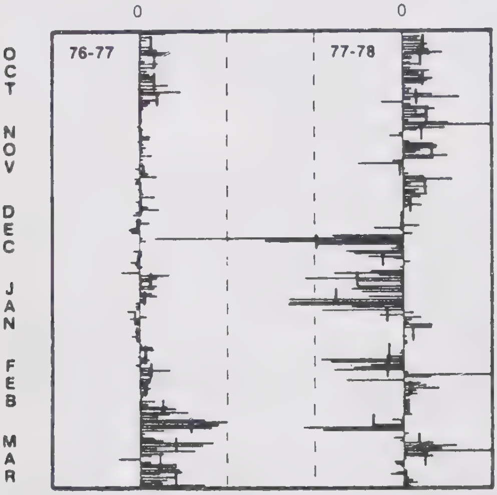

Figure 9. Daily and weekly means of 6-hourly upwelling index computations at 36 degrees N. latitude on the Central California coast. Horizontal lines indicate daily mean values. Values to the right of the zero line indicate offshore transport and upwelling; those to the left indicate onshore transport and downwelling.

Two very anomalous recent winter situations have been the winter of 1976-77, in which the near absence of storms contributed to a serious drought in California, and the winter of 1977-78 in which the drought was broken dramatically by unusually intense winter storm activity. Upwelling index computations (Figure 9) illustrate the contrasting conditions. The winter of 1976-77 is a consistently low energy situation marked by the near absence of periods of transport either toward or away from the coast. This lack of significant transport events is unique in the time series of daily indices which begins in 1967 (Bakun, 1975). During 1977-78 intense storm events followed one another in rapid succession, resulting in a highly fluctuating mixture of strong onshore and offshore transport episodes.

During the summer of 1977 extraordinary concentrations of juvenile rockfish were observed off northern[6], central[6], and southern California[7]. In contrast, the 1978 year-class appears to be a complete bust, judging from observations of summer juvenile concentrations[8].

To attribute the apparent differences in larval rockfish survival to the difference in transport conditions, it seems necessary to assume that the ability of larvae to maintain a position relative to the coast throughout the pelagic period is crucial. The extent to which the larvae may be capable of maintaining such a position is undocumented. Parrish, et al. (MS) point out a pattern of correspondence between fish reproductive strategies and transport characteristics which suggest a general difficulty in maintaining resident populations in the region of intense upwelling. If the relative success of the large number of rockfish species in countering this pattern is based on their livebearing mode of reproduction, the required assumption seems the most likely mechanism. It will be interesting to note whether the present very stormy winter, 1979-80, will be followed this coming summer by a scarcity of juvenile rockfish in California coastal waters.

6. Personal communication, Jim Hank, California Dept. of Fish and Game, Monterey, California, 93940.

7. Personal communication, Kenneth Mais, California Dept. of Fish and Game, Long Beach, California, 90801.

8. Personal communication, William H. Lenarz, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Tiburon, California, 94920.

Dungeness crab

Peterson (1973) found significant correlations indicating increased Dungeness crab landings off Washington, Oregon and Northern California in years following high values of Bakun's (1973) upwelling indices averaged over the spring and summer seasons. The lag times for the correlations were 1/2 year for Washington and 1 1/2 years for Oregon and Northern California. Since the period of growth from larva to recruitment is four years, the upwelling effect on recruitment could not be acting at the larval stages. Peterson suggested that delays in molting during years of low upwelling-related productivity could be the causative mechanism. However, the data do not appear to support this mechanism. Crabs cannot delay their molts indefinitely and one would expect a pattern of increased catches in the year following as the "delayed-molting" crabs reached harvestable size. This pattern is not evident. Rather, multi-year runs of good or poor catches dominate the available time series.

Botsford and Wickham (1975) using slightly different statistical techniques confirmed Peterson's results of significant correlation at lag times near one year. Their cross correlations were positive for lags extending out to the four year growth period, but not significant at the levels required to confidently reject the null hypothesis of no relationship. They hypothesize density dependent biotic factors, such as cannibalism of adults upon juveniles, as mechanisms for the observed long period cyclic variations.

These studies were done using upwelling index data through 1971 reported by Bakun (1973). More recent upwelling index computations have indicated an unprecedented series of very high spring and summer values beginning in 1973 and continuing through 1975. The crab correlation reported by Peterson appears to be continuing to hold with northern California landings rising explosively from 160 MT during the 1973-74 season, to nearly 700 MT in 1974-75, to over 6,000 MT in 1975-76, and to over 11,000 MT in 1976-77 (Orcutt, 1978). A drop to about 6,000 MT in 1977-78 may reflect slightly lessened seasonal upwelling index values for 1976 or perhaps the density dependent biotic factors suggested by Botsford and Wickham.

The Dungeness crab fishery in central California was appreciable through the 1960's but catches dropped to a low value in 1962 and have remained near that value ever since (Orcutt, 1978). Attempts to link the collapse to pollutants derived from human activities have been inconclusive (Wild, Hauger,'and Horn, 1978). Wild and Haugen (1977) have shown a significant correlation between sea level values during the fall and winter and crab landings three years later. This is the proper season and time lag for the relationship to reflect an effect on spawning success, possibly through the linkage of sea level to temperature. Laboratory studies have shown deterioration of egg masses at warmer temperatures (Wild, Hagen and Horn, 1978). The period analyzed in the regression covers the collapse of the fishery and a period of secular rise in sea level, although the authors point out that the highest correlations found are at the expected season and time lag rather than at all seasons and lags as would be expected if the correlations were controlled by the long term trends. This analysis is one in which a test of the correlation after high pass filtering of both the catches and sea level values would seem to be very helpful for interpretation.

Coho salmon

Gunsolus (1978) has indicated a relationship between seasonal upwelling index values off Oregon and both survival of juvenile coho salmon in their first year and the ultimate size of adults present that same year. Both survival rates and growth increase with indication of increased upwelling.

Further work by Zirges[9] suggests that the date of transition from the winter situation of generally negative daily values (Bakun, 1975) off Oregon to the positive values characteristic of spring and summer may be more directly related to survival than the seasonal average of the index values. The effect of upwelling on the direction of the local alongshore current flow could be the causative factor: after transition the predominant flow switches abruptly from poleward to equaterward (Huyer, Sobey and Smith, 1979). Another possible mechanism is that early transition would allow a larger fraction of the smolts leaving the rivers to experience the higher food particle concentrations resulting from upwelling-related primary production.

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9. Personal communication, Mac Zirges, Oregon Department of Fish and Wildlife, Newport, Oregon, 97365.

This result is pertinent to a controversy over the growing number of private salmon hatcheries being established in the region. If the indicated relationship reflects some sort of food-limited carrying capacity for salmon smolts in the ocean, then additional production should perhaps be discouraged. However, if the indicated relationship represents a control of the proportion of smelts surviving, rather than on the absolute numbers surviving, a limitation of production at present levels would not be warranted. Such a proportional control would be more likely if the effect of current direction were predominant or alternatively, if the linkage to upwelling were through size-dependent mortality interacting with growth rates dependent on upwelling-produced particle concentrations.

SUMMARY AND CONCLUSIONS

In defining the effect of the environment on fishery stocks we must deal with a space-time continuum of processes; the necessary coverage is generally not available from research vessel operations. Recently progress has been made using routinely collected maritime and shore station data to produce indicators of variations in important environmental processes. These have led to empirical studies of recruitment variations in certain California Current fishery stocks.

The studies have shed a certain amount of light on processes controlling fish stock fluctuations but have been information-limited. The empirical models based on the studies are not expected to be extraordinarily reliable or skillful in detailed prediction and simulation. However, they at least provide some indication of the tendencies created by environmental variability; they allow simulations of management strategies to at least incorporate a realistic spectrum of environmental variance.

Fishery management science is far from an exact science at this time. Present methods to incorporate environmental effects share this lack of exactness. However, experience has shown that ignoring the problem is no answer. Certainly, it would make little sense to attempt to manage the Peruvian anchoveta fishery without reference to El Nino occurences. Even as basic a fishery management concept as surplus production can become pretty nebulous in the face of major environmental perturbation; for example, Clark (1977) has suggested the possibility that the collapse of the anchoveta stock, which coincided with the 1972 El Nino, could have been due to insufficient fishing in 1971 as well as to excessive fishing in 1972.

The requirements for further progress are easily stated. We need more independent data points to provide additional degrees of freedom for the empirical approach and/or we need a better understanding of the processes linking fish stocks to their environment for advances via the rational approach. The two approaches are in many ways complementary. A better rational understanding would allow us to predetermine the shape and properties of the function which will be fitted to the available data points. More data points will allow a better and more detailed fit which would reveal more aspects of the functional relationship and thereby lead to increased understanding of the actual processes involved.

Since independent estimates of year-class strength of a given stock are available only once per year, increase of data points is a slow process. Substantial improvement in statistical significance comes only when degrees of freedom are at least doubled or tripled. Thus, in cases where we have several decades of information, simply waiting for more data to accumulate is not a useful response to present needs. However, where we may have only several years of data or no data at all, significant empirical advances would be possible in a reasonable time frame. In any case, when monitoring activities are needed, the best time to begin is immediately. Of course, our conception of what characteristics need to be monitored is always based on our rational understanding of the processes involved; thus substantial data accumulations are always based on a previous conception which is often altered as the data yield improved insight.

One development which may be capable of dramatically increasing the number of independent data points for larval survival processes is the technique of counting daily growth rings on larval otoliths

(Methot and Kramer, 1979). If larvae collected at sea can be effectively aged and their birthdates precisely fixed, the condition and abundance of larvae can be related to short term environmental conditions occurring between birth and collection. Thus, multiple independent data points on larval survival might be established in a single year. The technique appears to be quite labor-intensive, but expenditure in such a pertinent area may be preferable to dissipation of an equivalent amount of effort on activities which, although less tedious, may be less central to the management problem.

Substantial progress in the rational understanding sector likewise does not come easily. It is incredibly difficult to reproduce actual ocean conditions in laboratory experiments. Experiments at sea are also fraught with difficulties. The mixture of scales of motion at sea make it impossible to observe time-dependent aspects of any defined "parcel" of organisms and associated environment without artificially confining it somehow, which represents a fundamental alteration of conditions. Likewise, the actual processes tend to occur on such small space scales that it may be nearly impossible to make observations without perturbing the process being observed. However, the work of Lasker, Hunter, Theilacker and others, on larval anchovy survival processes, has shown that a well-conceived and painstakingly executed series of laboratory and field experiments can yield exciting breakthroughs.

Sometimes this process can be shortcut to yield certain limited results by simply comparing seasonal and geographic features of fish reproductive strategies with corresponding seasonality and geography of environmental processes. When a pattern is recognized, deductions can be made as to which processes appear to control reproductive success. Parrish et al (MS), for example, assembled seasonal transport and wind curl distributions on a finer scale than hitherto available and noted a striking pattern of avoidance of offshore transport in the spawning habits of the most successful coastal fish stocks of the California Current region. This provides a rational basis for empirical attempts to relate anomalous offshore transport to decreased reproductive success.

Dynamic modelling is undoubtedly useful in clarifying conceptual understanding. Mathematical models provide the necessary "bookeeping" to test whether a given set of assumptions can lead to results which resemble reality. However they cannot generate, nor are they a substitute for, observational data. Their results can only reflect the information and assumptions which are put into their formulation. Mathematics cannot, for example, by itself inform us how far offshore larvae must be transported for their contribution to eventual recruitment to be seriously impaired.

The concept of comparative studies can perhaps be profitably extended to detailed comparisons among the major eastern boundary current regions. Similarities and differences in seasonality and geography of analogous environmental and biological features may lead to pattern recognition which will enhance our understanding of the controlling relationships. Of course such comparisons must be made with great care and be based on a commonality of data types. Because of the continuity of space-time coverage required, the environmental features must probably be defined largely by maritime and other routinely collected data. Specialized research cruises and experiments can illuminate certain aspects within limited time-space "windows". The setting of these "windows" within the larger seasonal-geographical framework is critical. For example, the recent CUEA studies need to be interpreted carefully when used to compare gross aspects of the three eastern boundary current regions in which they were made. In many ways the location off Oregon where the CUE-1 and CUE-2 experiments were made is probably an analog to the area off Portugal (Wooster, et al., 1976) rather than to Cape Blanc where JOINT-1 was situated. Cap Blanc may be a better analog to Cape Mendocino (Bakun, et al., 1974) in the California Current. The JOINT-II location off Peru shares certain aspects, such as apparent nonlocal generation of upwelling characteristics (Smith, 1978), with the upwelling region in the Gulf of Guinea (Bakun, 1977). Such comparative studies can also be thought of as relieving the problem of limited degrees of freedom. Empirical models of environment - fish stock interactions among analogous stocks in the various regions can be compared for similarities and differences. If close enough analogies are indicated, statistical confidence would increase for the relationships in each of the regions; for example, in the theoretical case of perfect analogs the degrees of freedom could be considered to be directly additive.

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AERIAL CENSUS OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, IN A REGION OF THE TEXAS COAST

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ABSTRACT

On five replicate aerial surveys in late March 1978, the bottlenose dolphin, *Tursiops truncatus,* herds were sighted and their numbers estimated in 21 strip transects flown across bays and channels between barrier islands and the coast from Port Aransas northeast to Matagorda, Texas. The transects were spaced at 4.63 km intervals and herds were scouted in about 800 m wide strips totaling 436 km in length, providing approximately 17% coverage of the area. On surveys 1-4 (survey 5 was excluded from population calculations because it was conducted in adverse weather) 133 bottlenose dolphin herds were sighted, containing an estimated 916 animals. Within these strips the mean heard size was 6.95 animals and mean herd density was $0.0947/\text{km}^2$, extrapolating to a population estimate of 1,319 dolphins and a density estimate of $0.752/\text{km}^2$ for the entire area. These figures are relatively high in contrast to recent studies in other environments. About half the herds were feeding and approximately one-third were traveling. Sightings were most frequent in ship channels, shallow areas inside barrier islands, and near shore. There were several sources of bias in our measurements, and we consider the results to be conservative.

In the waters under jurisdiction of the United States, live capture of marine mammals is now limited by law to those species that are used for public exhibition and scientific research. With the exception of certain pinnipeds, the greatest demand is for the bottlenose dolphin, *Tursiops truncatus* Montagu, the most tractable of the smaller cetaceans.

This recent management regime has generated a need for assessment of marine mammal stocks that consider population size and reproductive rates of potentially impacted species (Odell et al.[6]). Obviously, rigorous density estimates are an essential starting point for such studies, but despite the long history of a live fishery for bottlenose dolphins (Townsend 1914) there are scant population data on which to base management decisions (Odell 1975).

The majority of bottlenose dolphins that are readily available for capture dwell in the coastal and inland waterways of Florida and the other states bordering the Gulf of Mexico. In such environments several factors make *T. truncatus*, in contrast to pelagic odontocetes, ideally suited for synoptic studies from aircraft: many of the environments are semienclosed waters of limited dimensions, the herds are usually small thus individuals can be relatively accurately counted, and *T. truncatus* is generally the only small cetacean in the area and therefore easily identified. Accordingly, recent studies of bottlenose dolphins off the northern Gulf of Mexico and the Indian River area of Florida have used and refined aerial survey tactics and methods (Leatherwood et al. 1978; Leatherwood 1979; Leatherwood and Platter[7]; Odell and Reynolds[8]). Using similar procedures

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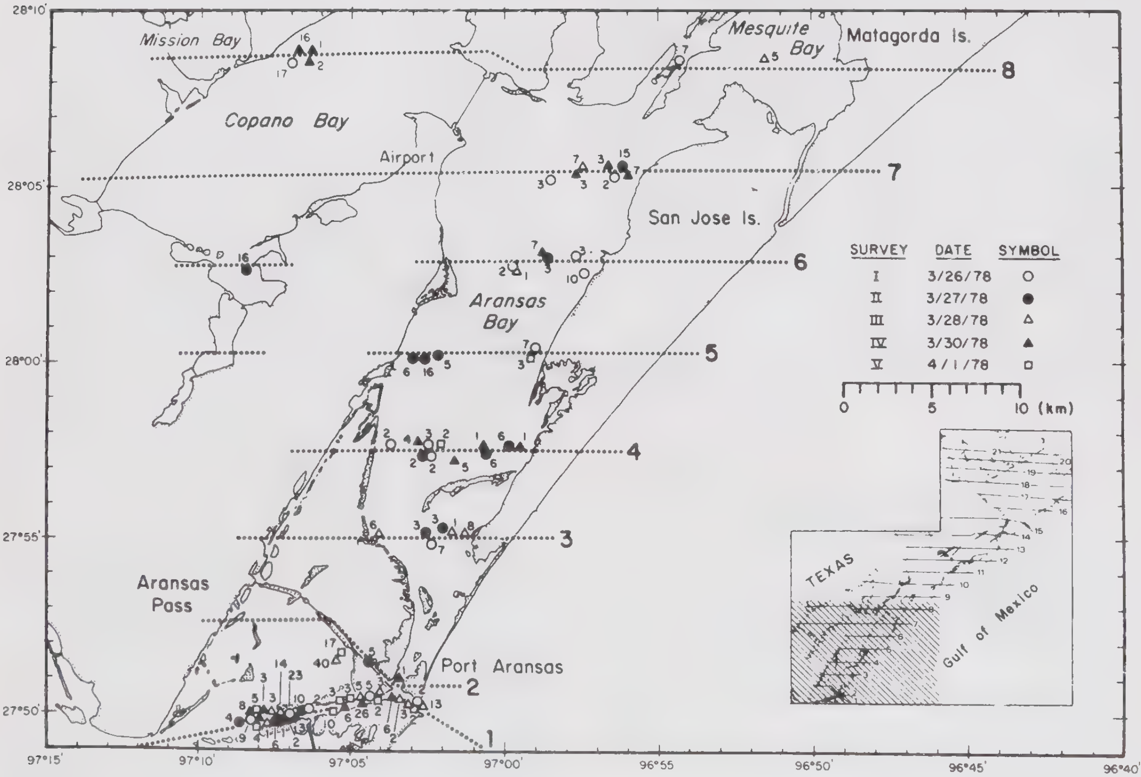
we report here on the size and density of the bottlenose dolphin population in the Port Aransas Pass-Matagorda Peninsula region of the Texas coast as observed in late March 1978 and compare the density figures with those obtained in the previous studies. Observations on *T. truncatus* distribution, behavior, sighting cues, and the perpendicular distances of the sightings, and alternative procedures and results are also presented and discussed.

STUDY AREA AND METHODS

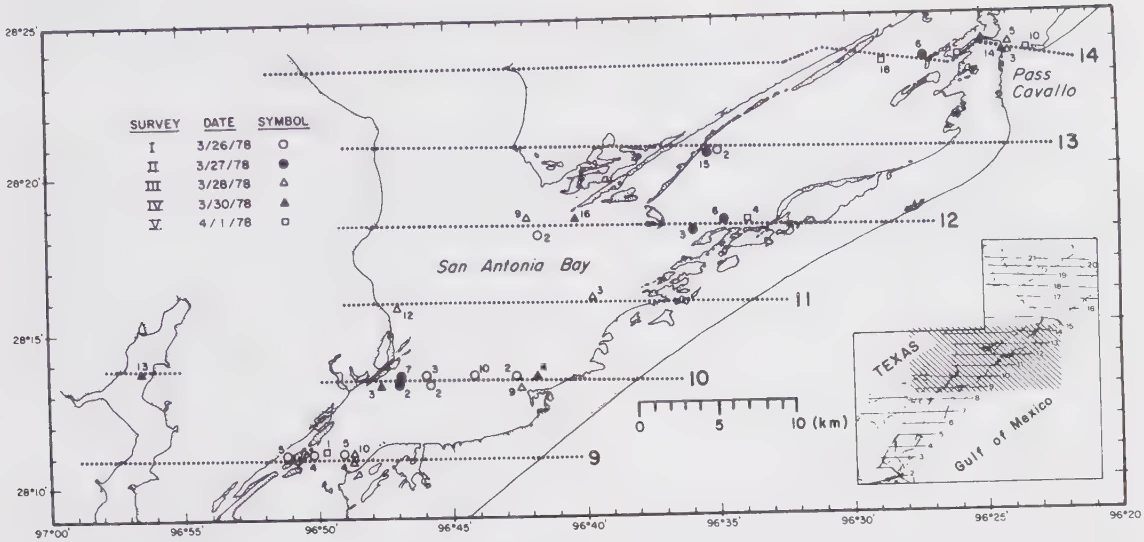
Based on previous research (Leatherwood et al. 1978), a strip transect was designed (Eberhardt 1978). The dolphin herds were sighted and their numbers estimated within strips theoretically 804.5 m wide (0.435 n.mi.). All sightings, regardless of the numbers of animals, were statistically considered as a herd, and the term is used here in the general sense of a grouping of animals without implying more complex behavior. To achieve precision the same area was surveyed during five replicate flights. The extent of the area surveyed was limited to dimensions that could be covered in 7-8 h of flying time and that would provide approximately 17% coverage of the area on any one replicate survey.

The surveyed territory extended along 160 km (86 n.mi.) of the central Texas coast from Port Aransas at the northern end of Corpus Christi Bay to the base of the Matagorda Peninsula (Figures 1-3). This terrain is a complex of bays, bayous, lakes, and channels bordered seaward by long, low barrier islands. Convoluted arms of the larger bays extend inland into river deltas surrounded by agricultural lands. Marshes fringe much of the barrier and outer bay shorelines and numerous sand and shell reefs, small islands, and spoil dumps interrupt the water areas. Extensive shoals are covered by water of <1 m, and the deeper parts of the bays are limited to about 4 m depths. Oil well platforms and well heads are numerous in some parts of the bays and man-made



28°10'
28°05'
28°00'
27°55'
27°50'
97°15'
97°10'
97°05'
97°00'
96°55'
96°50'
96°45'
96°40'
Mission Bay
Copano Bay
Airport
Mesquite Bay
Matagorda Is.
San Jose Is.
Aransas Bay
Aransas Pass
Port Aransas
1
2
3
4
5
6
7
8
SURVEY DATE SYMBOL
I 3/26/78 ○
II 3/27/78 ●
III 3/28/78 △
IV 3/30/78 ▲
V 4/1/78 □
0 5 10 (km)
TEXAS
Gulf of Mexico

FIGURE 1.—Distribution of bottlenose dolphin herds and their estimated numbers from Aransas Pass to Mesquite Bay (transects 1-8), Texas.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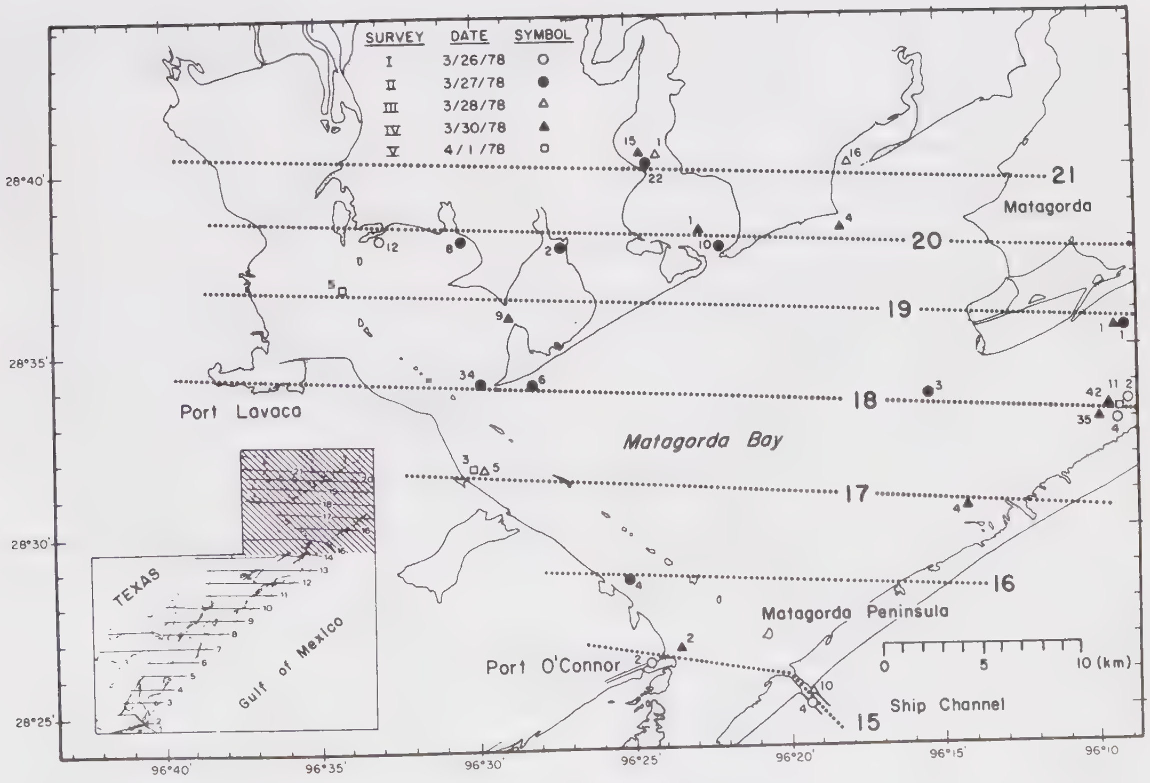
San Antonia Bay
Pass Cavallo
TEXAS
Gulf of Mexico
0 5 10 (km)
9
10
11
12
13
14
28°25'
28°20'
28°15'
28°10'
97°00'
96°55'
96°50'
96°45'
96°40'
96°35'
96°30'
96°25'
96°20

FIGURE 2.—Distribution of bottlenose dolphin herds and their estimated numbers from Ayres Bay to Pass Cavallo (transects 9-14), Texas.


SURVEY DATE SYMBOL
I 3/26/78 ○
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IV 3/30/78 ▲
V 4/1/78 □
Matagorda
Port Lavaca
Matagorda Bay
Matagorda Peninsula
Port O'Connor
Ship Channel
TEXAS
Gulf of Mexico
0 5 10 (km)
15
16
17
18
19
20
21
28°40'
28°35'
28°30'
28°25'
96°40'
96°35'
96°30'
96°25'
96°20'
96°15'
96°10'

FIGURE 3.—Distribution of bottlenose dolphin herds and their estimated numbers from Port O'Connor ship channel to Tres Palacios Bay (transects 15-21), Texas.

cuts and channels run through the area. Five channels, two man-made, open to the Gulf of Mexico.

Operating from Aransas County Airport, a high-wing, four-seat airplane was flown along 21 transect lines spaced at approximately 4.63 km (2.5 n.mi.) intervels across the study area (Figures 1-3). With some exceptions the transect lines were oriented due east to west. To provide a reference point with a previous population study (Shane 1977) the first two lines were bent to conform to the narrow Corpus Christi and Aransas ship channels (Figure 1). Line 8 was jogged slightly to the north over the Lamar Peninsula so that its western extension would cross Mission Bay (Figure 1). Lines 14 and 15 were altered to overfly the Pass Cavallo and ship channel entrances into Matagorda Bay in the region of Port O'Connor, the location of a proposed *T. truncatus* study. In 12 cases the transects were interrupted by land that divided them into two or more parts, so that in all, 42 overwater crossings were flown. Eight of these crossings were 2 km or less in length while the longest was 42 km. Their average length was 10.2 km. Time of these crossings ranged from <1 to about 18 min.

Most transects were flown at 167 km/h and an altitude of approximately 152 m (500 ft). The first part of transect 1 was flown at 213 m (700 ft) to safely maneuver around large cranes and other structures. When not fully occupied with flying the plane, the pilot searched for bottlenose dolphins. An observer sat in the right front seat next to the pilot. This observer also functioned as the "navigator," talking the pilot onto transect landmarks, calling out the start and stop times for each transect, and charting the dolphin sightings. Two observers sat in the rear of the plane. The observer in the right seat mainly functioned as a recorder who kept a transect log noting the time of starting and ending of each transect and comments on visibility, weather, and other observations of interest. A sighting form was also kept in which was noted: the observer making the sighting, the nature of the observation which first alerted us to the presence of a dolphin herd, the sighting cue; the estimated numbers of adult animals and calves and their assumed behavior; and the estimated right angle, or perpendicular, distance of the sighted dolphin herds from the plane's track. While a strip transect design had been planned, the perpendicular distance estimations were essential for alternative dolphin density calculations utilizing line transect theory (Seber 1973). If time allowed, the herd configuration relative to the environment was also sketched.

Because of the low flying speed, the airplane was relatively quiet and voice communication between party members was feasible. The shortness of the transects and rest intervals between transect lines alleviated observer fatigue.

Observers searched outward to about 400 m (we estimated distances in yards). This distance was estimated with the aid of tape markings on the wing struts that had been calibrated against range marks on the landing strip. When a dolphin sighting was made, the pilot deviated from the transect line and usually orbited the herd twice while all observers counted the animals and noted the presence of calves. A consensus opinion was scored for these counts. Rarely only one circle was necessary, and on occasion three or more circuits were flown before the observers felt confident with the count. On occasion, individual animals or small herds could not be relocated and limited data based on the original sighting were logged.

Two observers worked all the flights, whereas one person was relieved as recorder-observer for the last three flights. The same pilot flew the plane on surveys 1-4. A different pilot took over on the last survey.

RESULTS

Operations

The survey design called for six replicate transect runs on successive days. The period of the operation (26 March-1 April 1978), however, was plagued by strong winds (33-46 km/h) that caused a 1-day postponement of survey 4, cancellation of survey 6, and affected the results of survey 5 to the extent that those data are of limited value (the specific effects of weather on the survey will be discussed later). Weather conditions were good to excellent on two runs, surveys 2 and 4, and marginal to fair on surveys 1 and 3. A malfunctioning airplane engine caused curtailment of the last three transects on survey 2. These were made up at the end of survey 4 under similar environmental conditions. A total of 436 track kilometers (235 n.mi.) was flown on each survey. Assuming a 402.25 m scan on each side of the aircraft, an area of 351 km^2 (102 n.mi.^{2}) was searched. With the 4.63 km transect line spacing, this would represent about 17% coverage of the survey area on any one replicate.

Dolphin Counts

During the first four survey flights 133 dolphin herds were sighted, containing an estimated 916 animals. A mean of 33.3 herd sightings per survey, composing 229 dolphins, was calculated for the four flights (Table 1). On survey 5, affected by adverse weather, only 19 herds estimated to contain 107 dolphins were sighted. Because these scores fell well below two standard deviations of the mean that was calculated for the first four replicates (Table 1), the results of survey 5 were excluded from our population calculations. Data from the last survey were used, however, for analyzing behavioral observations, sighting cues, and the perpendicular distances of dolphin herds from the trackline.

TABLE 1.—Bottlenose dolphin herd sightings, individuals, and calves estimated on surveys 1-4 Port Aransas to Matagorda, Texas.

Date (1978)	Survey number	Total no. of herds	Total no. of animals	Total no. of calves	Percent of calves
Mar. 26	1	36	175	17	9.7
Mar. 27[1]	2	36	260	17	6.5
Mar. 28	3	29	209	20	9.6
Mar. 30	4	32	272	31	11.4
Total		133	916	85	
Mean		33.3	229.0	21.3	9.3
SD		3.4	45.2	6.7	2.0

[1] The last four transects were run on March 30.

Calves

Among the animals sighted in surveys 1-4, some 85 were classified as calves, and they represented 9.3% of the total population observed (Table 1). Because the surveys were made just prior to the peak of the calving season, it was not always possible to differentiate between older calves of the year and young yearlings. Some 13 animals were in this questionable category.

Herd Size and Herd Density

While the estimated sizes of herds ranged from 1 to 42 animals, generally the aggregations were small. Groups of two and three *T. truncatus* represented the mode and composed 28.6% of all sightings, and 96 of the 133 sightings (72.2%) were composed of 7 or less animals (Figure 4).

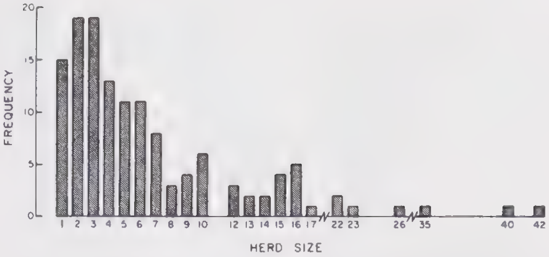

FIGURE 4.—Frequency distribution of bottlenose dolphin herd sizes on surveys 1-4, Port Aransas to Matagorda, Texas.

The mean herd size for each daily survey replicate was computed as:

$$\bar{h}_j = \sum_{i=1}^{n_j} \frac{h_{ij}}{n_j} \tag{1}$$

where $\bar{h}_j$ = mean herd size,
h_{ij} = herd size of the ith sighted herd on replicate j,
n_j = the number of herds sighted during replicate j.

The estimated herd density for each replicate was obtained from:

$$\hat{D}_j = \frac{n_j}{a} \tag{2}$$

where $\hat{D}_j$ = the estimated herd density on replicate j,
a = the surveyed area in km^2,
n_j = is defined as before.

These calculations produced a mean herd size of 6.95 and a mean herd density of 0.0947/km^2 (Table 2).

Estimated Population Size (Numbers of Dolphins)

In previous aerial assessments of bottlenose dolphin populations by Leatherwood and his coworkers, variance of the population size was calculated according to Goodman's (1960) equation for estimating the variance of a product of two independent variables. However, in these cases Goodman's equation was used to estimate variance of the mean population size over all the replicates

TABLE 2.—Basic terms and figures for population size and density estimates of bottlenose dolphin in the Texas bays resulting from replicate surveys 1-4.

Survey number (replicate)	Mean herd size ($\bar{h}_j$)	Variance mean herd size ($\mathrm{Var}\ \bar{h}_j$)	Herd density (no./km²) ($\hat{D}_j$)	No. of dolphins ($\hat{N}_j$)	Variance no. of dolphins[1] ($\mathrm{Var}\ \hat{N}_j$)	Dolphin density (no./km²) ($\hat{d}_j$)	Variance dolphin density[2] ($\mathrm{Var}\ \hat{d}_j$)
1	4.86	0.613	0.1026	1,008	58,828	0.575	0.0175
2	7.22	0.918	0.1026	1,498	100,613	0.854	0.0326
3	7.21	1.967	0.0826	1,204	103,000	0.685	0.0334
4	8.50	2.994	0.0912	1,567	175,232	0.893	0.0569
Mean	6.95		0.0947	1,319		0.752	
SD	1.52		0.0097	260.4		0.148	
SE	0.76		0.0049	130.2		0.074	
SE from theory					[3]189.43		[4]0.1080

[1]From Equation (9).
[2]From Equation (12).
[3]From Equation (10).
[4]From Equation (13).

and not the variances of each replicate. Quinn[9] has suggested a more refined treatment that is applicable if two conditions are met: the numbers of sightings for each replicate follows a Poisson distribution, and no real differences exist in the replicate herd densities. If these assumptions hold, a variance can then be legitimately computed for each replicate survey and these numbers pooled to produce a more precise estimate of mean population size variance. Accordingly, we proceeded as follows. The estimation of the population size for each replicate was calculated as:

$$\hat{N}_j = A\hat{D}_j\bar{h}_j \tag{3}$$

where $\hat{N}_j$ = estimated population size on replicate j,
A = total area assumed to be 5.76× of the searched area (a),
$\hat{D}_j$ = estimated herd density on replicate j,
$\bar{h}_j$ = mean herd size on replicate j.

Results are shown as "number of dolphins" in Table 2.

The computed variance of the estimated population size for each replicate was:

$$\mathrm{Var}\ \hat{N}_j = A^2\ \mathrm{Var}(\hat{D}_j\bar{h}_j) \tag{4}$$

which simplifies to:

$$\mathrm{Var}\ \hat{N}_j = \left(\frac{A}{a}\right)^2 \mathrm{Var}\ (n_j\bar{h}_j) \tag{5}$$

where a is assumed to be 17% of the total area (A).

The estimated variance of mean herd size within replicates was then estimated from:

$$\hat{\mathrm{Var}}\ \bar{h}_j = \sum_{i=1}^{n_j} \frac{(h_{ij} - \bar{h}_j)^2}{n_j\ (n_j - 1)}\ . \tag{6}$$

Following Elliott (1971), a chi-square value utilizing the index of dispersion was computed for the number of herd sightings on replicate surveys 1-4 to test agreement with a Poisson series. The index of dispersion was 0.35 with a resulting χ^2 value of 1.05. These values support the Poisson distribution assumption. This allows us to consider the variance of replicate herd sightings as equal to the numbers of herd sightings. Thus:

$$\hat{\mathrm{Var}}\ n_j = n_j. \tag{7}$$

Using the chi-square test again we also found that there was no difference at the 5% significance level in the herd densities of the replicate surveys. The mean herd size ($\bar{h}_j$) and the numbers of herds sighted (n_j), however, were obtained from the same set of observations, and as one reviewer has rightly pointed out, it is not known if in fact these estimates were independent. We therefore tested for interrelationship using Spearman's Rank Correlation Test (Zar 1974). Finding no demonstrable correlation at the 5% significance level, we proceeded to treat the results of the replicate surveys generated from Equation (5) in terms of Goodman's (1960) equation for estimating the variance of a product as suggested by Leatherwood et al. (1978). Thus:

$$\hat{\mathrm{Var}}\ \hat{N}_j =$$

$$5^2(n_j^2\ \hat{\mathrm{Var}}\ \bar{h}_j + \bar{h}_j^2\ \hat{\mathrm{Var}}\ n_j - \hat{\mathrm{Var}}\ n_j\ \hat{\mathrm{Var}}\ \bar{h}_j)\ , \tag{8}$$

and substitution of n_j for $\hat{\mathrm{Var}}\ n_j$ results in:

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[9] Terrance J. Quinn II, Center for Quantitative Science, University of Washington, Seattle, WA 98195, pers. commun. to S. Leatherwood, March 1978.

$$\hat{\text{V}}\text{ar}\,\hat{N}_j = 5^2(n_j^2\,\hat{\text{V}}\text{ar}\,\bar{h}_j + \bar{h}_j^2\,n_j - n_j\,\hat{\text{V}}\text{ar}\,\bar{h}_j)\ . \qquad (9)$$

Before proceeding, a one-way analysis of variance with unequal sample sizes was performed on herd sizes with a $\log_{10}$ transformation for counts. No significant differences ($\alpha = 0.05$) between replicate herd sizes were found, thereby allowing the pooling of the four variances as:

$$\hat{\text{V}}\text{ar}\,\bar{N} \doteq \hat{\text{V}}\text{ar}\left(\frac{\sum_{j=1}^{4}\hat{N}_j}{4}\right) = \left(\frac{1}{4}\right)^2 \sum_{j=1}^{4} \hat{\text{V}}\text{ar}\,(\hat{N}_j)\ . \qquad (10)$$

These computations produced an estimated mean *T. truncatus* population size of 1,319 with a standard error (SE) of 189 (Table 2).

The susceptibility of the above analysis to possible nonindependence of the mean herd size and herd density parameters was recognized by Leatherwood et al. (1978), and they suggested that mean herd size be established in preliminary flights before the herd counting phase of the survey is initiated. In the case of our work, however, because of inclement weather and limited resources we decided to make as many replicate surveys as possible rather than dividing the flight functions.

Despite the assurance of ranking tests, if independence between h_j and n_j does not hold, use of Equation (9) will probably underestimate the variance of N_j. An alternative more robust approach suggested by one reviewer was to compute the SE of the replicate estimates of numbers of dolphin on the four surveys (Table 2). This procedure produces a SE of 130.0 which is reasonably close to the theoretical value of 189 obtained from Equation (9) and tempers to some extent doubts of the validity of this approach.

Estimated Dolphin Density

For comparative purposes we also estimated the density of dolphins in the study area from:

$$\hat{d}_j = \hat{D}_j\bar{h}_j = \frac{n_j}{a}\bar{h}_j\ . \qquad (11)$$

The same rationale and procedures for calculating the replicate and overall variances of population estimates were used to calculate the variances for dolphin density. Thus:

$$\hat{\text{V}}\text{ar}\,\hat{d}_j = \frac{1}{a^2}(n_j^2\,\hat{\text{V}}\text{ar}\,\bar{h}_j + \bar{h}_j^2\,n_j - n_j\,\hat{\text{V}}\text{ar}\,\bar{h}_j) \qquad (12)$$

and

$$\hat{\text{V}}\text{ar}\,\hat{d} = \left(\frac{1}{4}\right)^2 \sum_{j=1}^{4} \hat{\text{V}}\text{ar}\,\hat{d}_j\ . \qquad (13)$$

This treatment gave an estimate of 0.752 dolphins/km^2 with an SE of 0.074. The SE calculated from the variance of the mean of the replicates was 0.108 (Table 2).

Comparisons with Other Population Studies

We can roughly compare our counts from the Aransas Pass area with those of Shane's (1977) who counted *T. truncatus* in the same area from a skiff run on a meandering course through the ship channels and cuts almost on a daily basis over a 1-yr period. For March and April 1977, her mean was 95 dolphins. The mean of our scores for transects 1 and 2 that covered part of her study area was 53. Considering the differences in methods and area covered, the results do not seem unreasonably diverse.

Our mean density estimate for all transects is compared with the results of recent aerial surveys of *T. truncatus* populations in waters adjacent to Florida, Mississippi, and Louisiana in Table 3. While it is clearly tenuous to contrast densities from different environments, it is worth noting that the two semienclosed areas, Indian River, Fla., and the Texas bays, appear to support similar densities, 0.52 dolphins/km^2 and 0.75 dolphins/km^2, respectively. The mean percent of the calves

TABLE 3.—Density estimates of bottlenose dolphin populations in southeastern U.S. coastal waters, based on recent aerial surveys. There are considerable differences in the nature and extent of the areas covered in these studies, thus the results are not strictly comparable.

Location	Reference	Dolphins per km^2	Dolphins per n.mi.^{2}
Florida			
Indian River	Leatherwood 1979	0.52	1.79
Florida[1] West coast	Odell and Reynolds (text footnote 8)	0.27	0.93
Mississippi Gulf coast	Leatherwood et al. (1978)	0.23	0.79
Louisiana Gulf coast	Leatherwood et al. (1978)	0.44	1.51
Texas			
Gulf coast	This paper	0.75	2.57

[1] Derived from their table 10 by computing the product of mean herd size (5.43) and mean herd density (0.0497).

to the total number of animals counted (9.3±2.0%) is about the same as previously reported (Leatherwood 1979).

Distribution and Behavior

As can be seen from Figures 1-3 the distribution of dolphin herds in the area was hardly homogenous. Some 28 herds (21%) of the total were sighted in the narrow Aransas Pass ship channels (mainly transect 1) and 211 (23%) of the animals counted were in these herds. (This marked difference in densities is discussed below.) Transect 18 across Matagorda Bay was another area of high dolphin density. While we noted only eight herds on this line they were relatively large and accounted for 14% of the dolphins sighted. In general, aside from the ship channels, the shoreward side of the barrier islands and locations close to the beach appeared to be favorable situations for *T. truncatus*, whereas sightings were rare in the middle of large bays.

When possible, the apparent behavior of the herds was coded as either traveling, playing, feeding, or resting. Of the 97 herds classified, about half (48.5%) were considered to be feeding. Side or upside down swimming by dolphins actively pursuing prey as reported by Leatherwood (1975) was frequently observed. This was particularly true in the shallow regions inside the barrier islands where Gunter (1954) reported that bottlenose dolphins frequently chase mullet, *Mugil cephalus*. Feeding appeared to be associated with herd size, for of the 17 herds composed of 15 or more individuals, 13 (76.5%) were considered to be feeding. The next most common behavior was "traveling," and 36 herds (37.1%) were assigned to that behavioral mode.

Perpendicular Sighting Distances and Sighting Cues

As previously indicated, in most cases we estimated the perpendicular distance from the plane's track to the sighted herd. In addition we also logged the nature of the observation which first alerted us to the presence of a dolphin herd, the "sighting cue" (Figure 5). During the field work, 11 different codes were used but these could be reduced to four classes: 1) surface perturbations such as mud trails or boils, scars, and splashes; 2) an animal's body seen below the water (most easily noted when the dolphins are rolling or swimming upside down and their contrasting light ventral surfaces are showing); 3) an animal's body, or part of it, or its condensed respiratory exhalation "blow" noted above the water surface; and 4) "cue uncertain or unnoted."

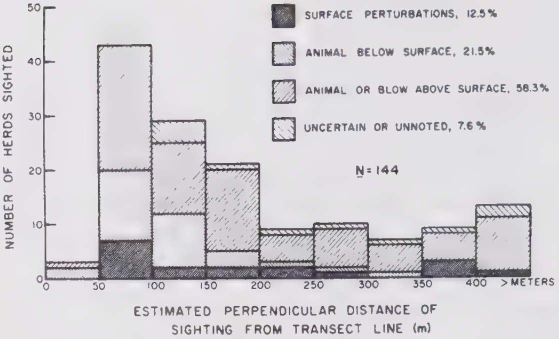

FIGURE 5.—Frequency distribution of estimated perpendicular distances of bottlenose dolphin herd sightings from transect lines on surveys 1-5, Port Aransas to Matagorda, Texas. Histograms are divided into the relative ratios of sighting cue classes.

The "animal above surface" cue was effective at all ranges and was the predominant sighting cue, accounting for 58.3% of all sightings (Figure 5). The "animal below surface" instigated 21.5% of the sightings, but was more important at ranges under 200 m, contributing 28 of the 96 sightings (29.2%) at these ranges, whereas, at ranges >200 m, only 3 of 48 sightings (6.2%) were signaled by this cue. As will be discussed later, the effectiveness of both underwater sightings and surface perturbations appeared to be vulnerable to weather conditions. Most questionable or unrecorded sighting cues occurred on the initial survey.

DISCUSSION

Possible Biases to Population Estimates

Several factors, both operational and analytical, influenced the results, in some cases prejudicing the counts upward and in others to lowering them. We first discuss two factors, effects of weather and inability to sight all herds, that tended to cause underestimates.

Relatively strong southwest winds (22-41 km/h) blew constantly for several days during the field operations. The wind's major effect on searching efficiency was not sea state, as is the case in the open ocean, for splashes were seldom the sighting cue, but rather the stirring of bottom materials into suspension creating large areas of highly turbid water. On such days the only clear water was in the lee of barrier islands and headlands where the fetch was limited.

Increased turbidity limits the observer's chances of sighting underwater animals and noting mud boils and trails. For underwater animals, however, the overall effect on the number of sightings was tempered because submerged dolphins will frequently be spotted when they eventually surface. More important was the negative influence of high turbidity on the observer's ability to note surface signs. For example, on the two low-wind days 12 out of 68 (17.7%) sightings were cued by surface perturbations. In contrast, on the three medium to high-wind days only 8 of 83 (9.6%) of sightings were signaled by this cue. The effect was probably more important than those data indicate, for frequently the observer's attention was drawn to an area by subtle surface signs and then, if a dolphin's body showed at the surface, it was usually the second rather than the first cue that was logged. As stated earlier, we have reduced the effects of weather on the population estimates by excluding the results of survey 5, when the wind effects were extreme, from the density computations.

Regarding our inability to sight all herds, the supposition that all target animals will be seen is basic to the strip transect method (Eberhardt 1978). However, in terms of line transect theory (Seber 1973), which assumes that the herds will be randomly distributed, the frequency histogram of the estimated perpendicular sighting distances (Figure 5) gives strong evidence that one of these assumptions was incorrect, probably the former, as follows. First, only 3 of 144 sightings were made at under 50 m range. The aircraft's configuration which severly limits searching the water directly under and adjacent to the flight path was the major cause of this discrepancy. (A secondary factor was discomfort to the observer's neck caused by attempting to look down at a steep angle.) The only sightings made directly under or close to the track were when the aircraft was in a steep turn, and frequently herds were noted at moderate ranges when we were circling on a previous sighting. Secondly, the systematic decrease of the sighting frequencies from 50 to 200 m, suggesting a negative exponential curve, and the "tail" out to 400 m must at least in part reflect the inherent inefficiency of the observers to see beneath the water's surface at low angles or to detect relatively small, low-contrast objects at even moderate distances.

Three factors, dolphin movement, nature of the terrain, and observer experience, may have had mixed effects on the estimates, as follows.

Regarding effects of dolphin movement between the open Gulf of Mexico and the bay behind the barrier islands, it was originally planned that volunteer observers stationed adjacent to the passes would note the numbers and directional movements of bottlenose dolphins during the hours of the survey. However, a week's delay in starting the field work and the subsequent resumption of college classes following Easter vacation made it necessary to cancel that observational phase. At the termination of survey 4, however, we flew homeward just outside Matagorda Peninsula and Island. Outside Pass Cavallo at least 50 *T. truncatus* were seen loiling in small herds in and just outside the surf zone. These dolphins may have either been moving in from the Gulf or out of the bays, but their proximity to the beach and the pass indicates that there was frequent movement of dolphins between the two environments.

Factors of bathymetry of the bays and the nature of the terrain were not considered by the analysis. While *T. truncatus* were occasionally noted in shallow water just inside the barrier islands, extensive regions in the middle of the bays and in the shoreward areas were covered with a thin layer of water over sand and mud flats and there are numerous reefs and islands. Thus, within most of the 800 m swaths used to compute the density estimates there was territory that was not available to the dolphins that could legitimately be subtracted from the area searched. On the other hand, by multiplying the searched area by 5.76 (Equation (3)) to obtain an estimate of the total number of dolphins we were sometimes attributing dolphin habitat to dry land. This is particularly true for the Port Aransas ship channels that were limited to about 600 m width and were surrounded by large land areas.

We feel that observer experience possibly also biased the accounts. *Tursiops truncatus* herds appear to occupy a home range (Caldwell 1955; Shane 1977) and we frequently sighted herds that were of similar size and in the same approximate location of herds noted on previous surveys. The observers tended to concentrate their attention on these areas and thus searched them more efficiently in the latter surveys.

Despite the smallness of the herds, it was not easy to accurately count animals that were sometimes spread over a relatively large area, and in subgroups that only showed for brief periods at the surface. Obviously, accuracy of such counts will also improve with experience. However, by scoring a consensus opinion the judgment and bias of the most experienced observer probably carried more weight, and as a result we feel that in all cases the counts were conservative. Because of the experience factor we also think that, other influences being equal, the latter surveys were probably the more accurate.

Last, one factor, the "gerrymandered" lines of transects 1 and 2, clearly tended to influence the counts upward. Our rationale for altering the line of these transects was based on the desirability of obtaining data in an area for which baseline information already was available (Shane 1977). Unfortunately, the terrain was not ideal for transect sampling, and flying an east-west line over the ship channels would have resulted in gross underestimation of an area known to hold a relatively large number of dolphins.

Clearly, the results for transects 1 and 2 (23% of the animals sighted in only 6.6% of the total area) were strikingly different from those data for the rest of the transects. Estimated dolphin density for the ship channels was 2.633/km^2, some 4.25 times greater than the 0.619/km^2 estimated for transects 3-21 (Table 4). Based on these densities the total population estimate could be partitioned into 304 dolphins for the ship channels and 1,015 animals in the rest of the area. Shane's (1977) maximum estimate for the ship channel area for any month of the year was about 280, thus the two estimates are in reasonable agreement. We still feel, however, that there were some unresolvable problems with our survey methodology as it applied to the Aransas Pass ship channels, and that the soundest procedure was to lump the results from the minority area with those from the major region, as we have done.

Alternative Density Estimate

As previously discussed, the decrease in the number of dolphin sightings at increasing ranges of the herds from the flight path (Figure 5) indicated violation of strip transect theory assumption that all herds within the delineated area were sighted. Line transect theory (Seber 1973) provided an alternative method of analyzing the results. Because there were few observations in the 0-50 m increment, creating a marked gap in the frequency distribution, and the "tail" of the frequency distribution was truncated, in part because we limited observations to about 400 m range, our data were not strictly applicable to line transect theory, either. Despite these discrepancies, however, we obtained for comparative purposes a rough approximation of the level of bias by applying a simple modification of the so-called exponential estimator (Gates et al. 1968) which corrects for the gap in the 0-50 m frequency distribution interval as follows:

TABLE 4.—The basic terms and figures for comparing the estimated bottlenose dolphin density in two parts of the survey, the Port Aransas ship channels (transects 1 and 2) and rest of the area (transects 3 to 21).

Survey number (replicate)	Total no. of herds	Total no. of animals	Mean herd size ($\hat{h}_j$)	Herd density no./km^2) ($\hat{D}_j$)	Dolphin density (no./km^2) ($\hat{d}_j$)	Variance dolphin density ($\hat{\mathrm{V}}\mathrm{ar}\ \hat{d}_j$)
Transects 1 and 2						
1	5	41	8.20	0.2165	2.045	1.6005
2	8	35	4.38	0.3465	1.749	0.5162
3	8	84	10.50	0.3465	4.191	5.0629
4	7	51	7.29	0.3032	2.546	2.0490
Total	28	211				
Mean	7	52.6	7.59	0.3032	2.633	
SD	1.4	21.9	2.53	0.0613	1.090	
SE	0.7	10.9	1.27	0.0307	0.545	
SE[1]						0.8750
Transects 3 to 21						
1	31	134	4.32	0.0946	0.471	0.0121
2	28	225	8.04	0.0854	0.791	0.0350
3	21	125	5.95	0.0641	0.439	0.0133
4	25	221	8.84	0.0763	0.776	0.0552
Total	105	705				
Mean	26.3	176.3	6.79	0.0801	0.619	
SD	4.3	54.1	2.05	0.0130	0.190	
SE	2.1	27.0	1.03	0.0065	0.095	
SE[1]						0.0980

[1] From Equation (13).

$$\hat{d} = \frac{n}{2L(\bar{Y} - 0.05)} \qquad (14)$$

where $\hat{d}$ = estimated dolphin density,
n = total number of dolphin sightings,
L = length of the track line in km,
Y = mean perpendicular sighting distance (minus the 50 m gap).

These calculations gave a density estimate for herds of 0.28/km² compared with 0.095 for the strip transect method (Table 2), evidence that the latter method may have underestimated the dolphin density by about a factor of 3.

In conclusion, the relatively few sightings in the 0-50 m perpendicular distance interval and the exponential decrease in sightings at ranges >100 m, strongly indicate violation of the strip transect assumption that all herds within the delineated strip were noted. If this is true then the population has been underestimated to some degree, although the inclusion of transects 1 and 2 would tend to compensate for this. Conversely, one assumption of line transect theory is that the targets are randomly distributed. We found, however, that the distribution of the dolphin herds was strongly nonrandom. This factor may have caused an upward bias to those calculations, but the precise impact of this violation is presently unclear. These questions cannot be resolved until further surveys are done simultaneously with adequate "ground truth" counts.

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Radio Tracking of Dolphins in the Eastern Tropical Pacific Using VHF and HF Equipment

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Abstract — Radio tracking was used to study the dynamics of schools of dolphins involved in the yellowfin tuna fishery of the eastern tropical Pacific. Complete VHF and HF systems were assembled. The primary VHF system consisted of Model MK-IV transmitters by Telonics, Inc., a Model 320 automatic direction finder (ADFS) by Ocean Applied Research (OAR), and an OAR Model AA-380-400 Adcock Antenna. The primary HF system was based on OAR AB-245 transmitters, an OAR ADFS 210 receiver, and an OAR AA-270-400 Adcock antenna. Secondary components were assembled for both systems.

The VHF system proved most reliable in allowing three two-day tracking sequences over 90.7, 19.1 and 120.9 nautical miles. Maximum range of the VHF system was 9.2 ± 0.2 nautical miles or 14.7 ± 0.3 nautical miles depending on the receiver. The dolphin schools showed a low degree of cohesion over the period of the study.

INTRODUCTION

The primary purpose of this paper is to assist other researchers to assemble radio tracking systems by briefly describing VHF and HF systems used to track dolphins in the ocean. A tracking system was essential to studies of school dynamics involving tagging, tracking, and recapture of dolphin schools to determine the degree of school integrity. Because other investigators consistently reported problems with malfunctions of components, particularly the transmitters, two complete tracking systems were assembled using VHF and HF.

The tracking was conducted from a commercial tuna purse seiner from 12 September to 31 October, 1978 during a two month research cruise in the eastern tropical Pacific near Clipperton Island. The dolphin schools were caught by the purse seiner during routine fishing operations. The dolphins were recovered from the net and maneuvered into a comparmentalized system of net corrals and aluminum cages with chutes where they were examined, radio and disc tagged, and released. The experimental design called for placing radio tags on one or two dolphins in the school during selected sets, tracking the school for 2 days, recapturing and reexamining the school. The sequence was to be repeated and the radio packs removed at the end of the experiment.

MATERIALS AND METHODS

The VHF system was the primary one used during the study. The transmitters were Model MK-IV by Telonics, Inc. which were cubical in shape, measuring approximately 6 × 4 × 3 cm and weighing 170 g. Transmissions were 30 ms pulses at a 0.6 s pulse rate with frequencies between 148.748 and 148.850 MHz. Power output was 0.25 W and the life expectancy was 2.5 months. These transmitters did not have a salt water switch. The antennas were 48 cm stainless steel whips insulated with a plastic sheath. The transmitters passed hydrostatic testing to 300 m, although the cases did deform slightly.

The principal receiver was a Model OAR ADFS 320 automatic direction finder (ADFS) manufactured by Ocean Applied Research (OAR) which had a signal 'lock and hold' capability. This feature allows the signal to be displayed for a longer period of time on the direction finder screen thereby facilitating tracking. An Adcock antenna, OAR Model AA-380-400, was used with the OAR ADFS 320 and was mounted on top of the crow's nest, placing it about 26 m above the sea surface. A preamplifier was used to improve the signal-to-noise ratio by providing an additional gain of 10 dB. Interfaced with the ADFS 320 was a Rustrak strip chart recorder for recording surfacing frequencies of the tracked dolphins.

A secondary VHF system was set up to relocate any animals lost by the other system. It consisted of a Telonics TR-2 receiver, an omnidirectional whip antenna, a three-element quad antenna which could be hand rotated to determine bearing, and an antenna switch box. The TR-2 receiver is more sensitive than the OAR ADFS 320 but is less convenient to use for longterm tracking. The audio output of the TR-2 could be connected to a cassette tape recorder to obtain surfacing rates.

The primary HF system was based on OAR AB-245 transmitters which consisted of two tubes, each measuring about 14 × 2 cm, rigidly connected into a U-shape. A 44.5 cm polyurethane jacketed top loaded whip antenna was mounted on the front piece directly between the transmitters so that it would be in line with the dorsal fin. The transmitters with batteries weighed 237 g, had an output of 0.60 W and frequencies of 27.585 and 27.595 MHz. A salt water switch regulated transmission by turning off the transmitter when submerged.

An OAR ADFS 210 was the primary receiver with another like it serving as a back-up. An Adcock antenna, Model OAR AA-270-400, was mounted approximately 10 m above the sea surface and was connected to the ADFS 210.

Saddles of Kydex plastic were molded from a cast of the dorsal fin and upper back of a typical adult male spotted dolphin, *Stenella attenuata*. The saddles were lined with 0.64 cm closed cell, neoprene rubber. The HF transmitters were attached directly to the saddles with rivets and plastic ties. The VHF transmitters were placed on one side of the saddle and an equal weight on the other side for balance. The VHF saddles were potted with two-part rigid polyurethane foam, hydrodynamically shaped with a slightly bulbous front. Individual variation in the saddles required custom fitting to each dolphin. With the saddle in place, a 0.64 cm diameter biopsy needle was used to bore a hole through the dorsal fin used to attach the saddle. A 0.64 cm diameter stainless steel bolt was inserted simultaneously as the biopsy needle was extracted to reduce bleeding. The bolt was covered with a sleeve of biocompatible nylon which was slightly larger than the hole, thereby serving as a compress to minimize bleeding. A corrosive magnesium nut was used to assure that the pack would be released if the animal was lost.

Once the animals were released, a 24 h tracking watch was started with particular attention paid to signal strength so that the transmitter would not get out of range, yet maintaining a minimum distance of 1.5 to 2.0 nautical miles to avoid influencing the dolphin's behavior. The watch was rotated on 2 h shifts.

RESULTS

Three radio tracking sequences were successfully conducted for total distances of 90.7, 19.1, and 120.9 nm. The first two sequences were of two-day duration and the third was in two legs of two days each. During the second sequence, the saddle broke off the bolt but because it was buoyant and balanced, the pack floated with the antenna upright and was retrieved.

Successful tracking only occurred with the VHF system. The only HF transmitter used malfunctioned almost immediately whereas the five VHF transmitters functioned reliably each time.

During the first tracking sequence, an adult female and adult male dolphin were radio tagged and released with their tagged school at 16.44. By 18.55 they were headed in different directions and the female was followed. At 21.32 the last signal was received from the male. During the last radio tracking sequence, two radio tagged animals were released with their tagged school of 101 dolphins. After two days of following one of the dolphins, it was caught with a group of 150 dolphins. Only one animal had a tag. A radio pack was placed on an adult male in the new group and tracked for two additional days. It was recaptured with 54 other dolphins, only 6 of which bore tags from the previous set.

Range tests at sea on the VHF transmitters indicated a maximum of 9.2 ± 0.2 nautical miles with the OAR ADFS 320, and 14.7 ± 0.3 nautical miles with the Telonics TR-2. Tests near the coast indicated a range of about 10 miles with the TR-2. No similar range tests were conducted for the HF gear.

CONCLUSIONS

The tracking system allowed a study to be conducted on dolphin school dynamics which indicated that there was little cohesion in these dolphin schools through a short-term period (2 days). The VHF system functioned reliably and permitted successful tracking of dolphins in the open ocean. An advantage of the VHF over HF system was that there was little or no interference in that frequency which facilitated tracking.

The saddles need to be improved for longer term tracking to minimize the abrasion noted during these studies. The polyurethane potting material became water-logged as did the neoprene saddle lining. Substitutes are needed for these purposes.

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PASSIVE BEHAVIOR BY THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN TUNA PURSE SEINE NETS

The purse seining method of catching yellowfin tuna, *Thunnus albacares*, in association with schools of dolphins in the eastern tropical Pacific has been described by Perrin (1969). The primary target species, in order of importance, are the spotted dolphin, *Stenella attenuata*, and the spinner dolphin, *S. longirostris*, with occasional net sets made on schools of the common dolphin, *Delphinus delphis*. Schools of these dolphins ranging in size from 50 to several thousand are herded with speedboats and encircled with a purse seine net that is from 900 to 1,400 m long and as much as 130 m deep. After the dolphins are encircled, the bottom of the net is pursed, entrapping the mammals and any tuna that are associated with the school. Presently, neither the mechanisms nor the function of the close association of the yellowfin tuna with these schools of dolphins in the eastern tropical Pacific are clearly understood.

Studies of the behavior of dolphins while captive in a purse seine net were pursued during the chartered cruise of the commercial seiner MV *Elizabeth C. J.*, in October 1976 (Norris et al.[1]). Prior to this cruise, however, beginning in 1973, an intensive effort was made to develop net modifications and fishing techniques that would decrease the incidental killing of the mammals. Much of this effort was based upon general, to date unpublished, observations of captured dolphins and tuna made by National Marine Fisheries Service (NMFS) observers and technologists. One of the behavioral patterns of the spotted dolphin first noted by NMFS divers in 1973 and then recognized for its contribution to incidental mortality in 1975 is termed here "passive" behavior.

In the fall of 1975, NMFS chartered the purse seiner MV *Bold Contender* to carry on fishing gear dynamics research aimed at reducing incidental dolphin mortality. Part of this research included the evaluation of the use of a two-man inflatable raft as a dolphin rescue platform during and after the release procedure known as the "backdown" (Perrin 1969; Coe and Sousa 1972). A face mask and snorkel were worn by the person in the rescue raft to enable him to: 1) signal when tuna were approaching the release area during backdown, 2) keep track of sharks, particularly the oceanic whitetip shark, *Carcharinus longimanus*, both inside and outside of the net, 3) locate and release any stray dolphins and, 4) observe the dynamics of the net modification being tested during the cruise. Notes on the behavior of the captured dolphins during backdown were recorded after each of the 25 net sets in which the rescue raft was used. The underwater passive behavior of spotted dolphins was first noted in the eighth net set of the cruise and in 14 subsequent sets.

The passive behavior manifests itself in possibly two forms during the backdown release procedure. The first, which has been described as "rafting" by Norris et al. (see footnote 1), consists of groups of 5-50 or more spotted dolphins hanging tail-down at or near the surface and showing no overt reactions to their surroundings. This type of passive behavior can be seen from the deck of the seiner and is generally displayed from the time the net is pursed through the backdown (about ½ h). There is a steady increase in the number of rafting animals until backdown begins and then an apparent sharp decrease as backdown proceeds. The decrease in rafting may be due to the crowding and confusion during that period. Rafting behavior simplifies the effective release of these animals by backdown, because the net is actually pulled out from under the "raft" of dolphins as it remains relatively stationary in the water. Observations during the *Elizabeth C. J.* cruise showed that in every school of captured spotted dolphins some portion exhibited this behavior.

Dolphins in the captured school that are not in rafts during backdown are either actively swimming, usually in the horizontal plane directly away from the advancing wall of the net, or display the second manifestation of passive behavior. Prior to backdown, rafting dolphins are occasionally observed to sink tail first to depths up to 5 m before they swim awkwardly back to the surface, breathe, and sink again. During backdown, however, there are occasionally relatively large numbers of animals that sink to lie on the webbing (Figure 1) and many more that show signs of the sinking behavior and drop out of the rafts.

During backdowns on the *Elizabeth C. J.* cruise, from 3 to an estimated 75 spotted dolphins and, in one set, 2 bottlenose dolphins, *Tursiops truncatus*, were observed lying on the webbing in the bottom of the backdown channel. These animals, which

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[1] Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna fishery - preliminary studies. Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as PB-283970, 86 p.

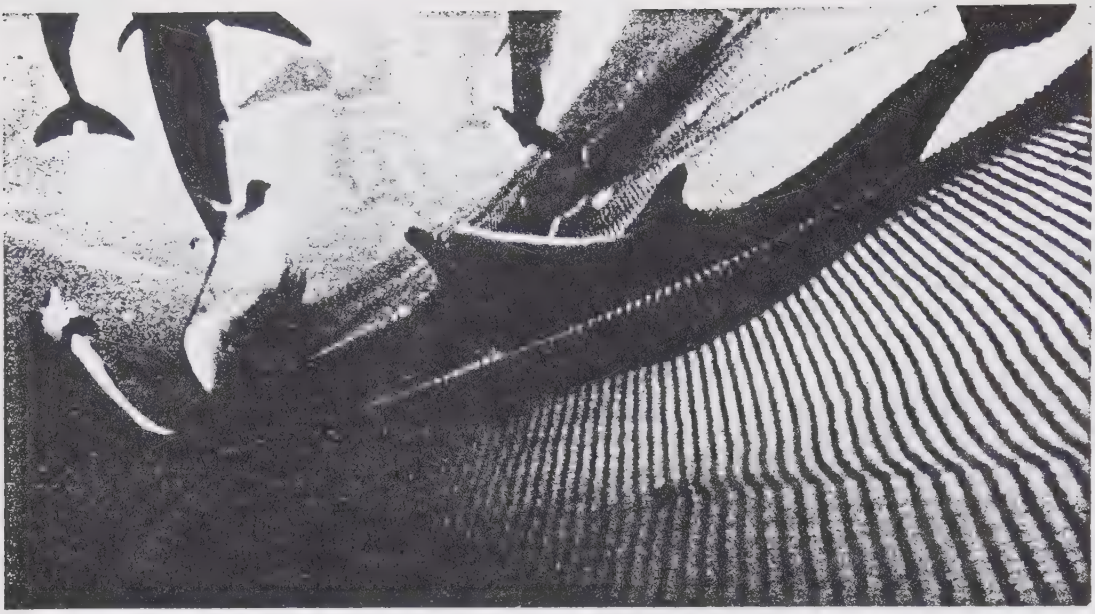

FIGURE 1.—Photograph taken during backdown of a tuna purse seiner showing three passive dolphins in the foreground. Note that the middle animal is resting on its dorsal fin. The four animals that are hanging flukes downward in the water are displaying the sinking behavior associated with rafting. (Photo courtesy of the Cooperative Dedicated Vessel Research Program, 1978.)

were making no apparent attempt to surface, were at depths that varied from 2 or 3 m to as much as 12 to 15 m. At first glance, the animals appeared to be struggling feebly, perhaps against the current being produced as the seine was pulled through the water during backdown. Their movements were weak and lacked the grace that long observation leads one to expect in dolphins. The majority of animals lying on the net in this manner were oriented with their heads toward the release area of the net (i.e., in the direction of the current), whereas the rafting and active animals were normally oriented away from the release area (i.e., heading into the current). After about 3-5 min, the passive dolphins began to rise singly or in two's and three's to breathe and were either backed out of the net or hand-released if the backdown procedure had already been terminated. No animals were seen returning to rest on the bottom of the net after surfacing.

Prior to promulgation and adoption of a federal regulation requiring use of a rescuer in a raft using a mask and snorkel, which resulted from the chartered cruise of the *Bold Contender*, this passive behavior probably was an important contributor to dolphin mortality in purse seines. When viewed from the deck of a speedboat tending the corkline in the dolphin-release area during backdown, these animals appeared to be dead if they were noticed at all, and as a result the release efforts were often prematurely terminated. Dolphins not released during the backdown have a high probability of being killed (Coe and DeBeer[2]).

The reasons for passive behavior in purse seine-caught spotted dolphins are not understood. The behavior has only rarely been observed in spinner dolphins in the tuna fishery. A similar behavior pattern has been described for two newly captured Hawaiian spinner dolphins during escape behavior experiments designed to delineate the dimensions of a dolphin release gate for possible use in purse seine nets (Perrin and Hunter 1972).

Animal trainers and biologists have noted what appears as similar behavior in individual captive dolphins of several species. Caldwell et al. (1966) reported prolonged inverted "resting or sleeping on the bottom of the tank" by a juvenile male Boutu, *Inia geoffrensis*. The occurrence of this behavior in *I. geoffrensis* and that observed in a juvenile male Atlantic bottlenose dolphin was frequent and apparently spontaneous (Caldwell[3]). Pryor[4] and Norris et al. (footnote 1) have noted instances where the passive-type behavior was presumably induced in training situations where *Tursiops* spp. were being "worked hard." These animals would go to the bottom of the tank, emit a quantity of air and might remain at the bottom for several minutes. Norris et al. hypothesized that this behavior may be similar to the "dearoused state" described by Delius (1970) for terrestrial animals, the most widely known example of which is the feigning of death by the Virginia opposum, *Didelphis marsupialis*. The major criticism (Norris et al.) of the dearousal hypothesis in the present situation would seem to concern the evolutionary value of such a response to a pelagic air breathing animal that would tend to sink toward the bottom in very deep water. One argument (Norris et al.) is that the situation which elicits dearousal (purse seining) has been a factor for only about 15-20 yr, and it is therefore not necessary to hypothesize an adaptive value for the behavior. To accept this hypothesis it would have to be assumed that the capability for dearousal has evolved in response to other circumstances.

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[2] Coe, J. M., and J. DeBeer. 1977. Results of the 1976 twenty vessel test of two fine mesh systems to reduce incidental porpoise mortality in tuna purse seining. Unpubl. manuscr., 75 p. Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

A second hypothesis to explain this behavior relates to the effects of chase and capture on the physiology of the dolphins. Possibly indicative is the awkwardness of the swimming movements displayed by the animals while "passive." Harthoorn (1973) described the effects of chase and capture on large African mammals. Long chases using motor-driven vehicles result in a typical condition termed "capture myopathy." Capture myopathy is very common in the animals captured for zoos and often causes a delayed mortality. Symptoms include stiffness and awkward movements. The method of capturing dolphin schools involves a chase by speedboats that lasts up to 1.5 h and averages between 20 and 30 min. A chase of that duration is capable of causing myopathies in large terrestrial mammals which can be detected by measuring changes in blood serum enzyme levels (Harthoorn). A recent paper by Colgrove (1978) documents a suspected case of myopathy in a dolphin, *Tursiops gilli* = *T. truncatus*. This case of myopathy appears to have been induced by the stress of transporting the animal. Investigation of blood chemistry of passive dolphins may allow determination of whether capture myopathy does occur as a result of chase and capture during the tuna seining operation.

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[3] David K. Caldwell, Director, Biocommunication and Marine Mammal Research Facility, University of Florida, Route 1, Box 121, St. Augustine, FL 32084, pers. commun. October 1979.

[4] Karen Pryor, former head animal trainer, Sea Life Park, Hawaii; present address: 28 East 10th Street, New York, NY 10003, pers. commun. November 1976.

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A multiple mark and recapture estimate applied to polar bears

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The mark–recapture technique described in this paper estimates polar bear (*Ursus maritimus*) populations for all sample periods except the first sample period, incorporates an open population model, and is supported by ecological data from ringed seals and polar bears. The estimation procedure requires that survival rates are either known or estimated independently as part of the research program. Reasonably precise estimates will be produced if 10 to 20% of the population can be marked and sample sizes of 150 bears can be handled at any given sample period.

DEMASTER, D. P., M. C. S. KINGSLEY et I. STIRLING. 1980. A multiple mark and recapture estimate applied to polar bears. Can. J. Zool. **58**: 633–638.

La technique de marquage–recapture décrite ici a permis l'estimation des populations d'ours polaires (*Ursus maritimus*) pour toutes les périodes d'échantillonnage sauf la première; elle inclut un modèle de population ouverte et est corroborée par des données écologiques sur des phoques annelés et des ours polaires. Le processus d'estimation suppose que les taux de survie sont connus ou estimés par d'autres moyens. La technique permet des estimés précis lorsque 10 ou 20% de la population peut être marquée et elle permet de traiter des échantillons de 150 ours en n'importe quelle période d'échantillonnage.

[Traduit par le journal]

Introduction

Estimating the sizes of populations where the individuals do not concentrate at any time of the year, and in which the probability of sighting is always less than unity, presents unique problems. Historically, population estimates of polar bears have involved strip transects (Tovey and Scott 1957), sustainable kill estimates, or mark–recapture techniques (Stirling et al. 1975). Of the three, the latter seems the most cost effective, in that along with population estimates, mark–recapture programs provide information concerning movements, rates of growth, reproduction, and survival. The major disadvantage of strip-transect methods for estimating the sizes of such low-density populations is the large effort that is usually required to produce usably narrow confidence intervals on a population estimate (Eberhardt 1978). Another problem associated with strip transects is that the probability of sighting free-ranging polar bears with aerial surveys is both low and difficult to evaluate. Estimation based on sustainable kill data is fraught with untestable assumptions and poorly understood relationships between regulatory mechanisms and harvest strategies (DeMaster 1978).

Mark–recapture estimates of numbers of polar bears have usually incorporated closed population models (e.g., the Lincoln–Peterson estimate (Stirling et al. 1975)). The major problem with this approach is that it involves a compromise between sample size and the closed population assumption. If movements in and out of an area can be assumed to be negligible, then births and survival must be 0 and 1.0, respectively. The time interval during which there are no births or deaths in the population requires that the entire sampling procedure be accomplished within a few months at the longest, and therefore, unless polar bear densities are high, the sample sizes associated with tagging polar bears are unmanageably small (see Stirling et al. 1975).

The Lincoln–Peterson estimate can also be used in an open population model if births and immigration are negligible and marked and unmarked animals have the same rates of mortality and emigration. In this case, the estimate is for the population size midway through the initial marking period. However, situations where influx is negligible, while egress is assumed to be important, seem unlikely. Gilbert (1976) reported that influx and egress of polar bears through a study area in Alaska were important factors in influencing the population estimates.

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The Seber–Jolly procedure (Seber 1973) is often used to avoid the assumptions of a closed population, but problems have arisen in estimating populations of polar bears with this method. Stirling et al. (1975) and Gilbert (1976) used this approach but found that the small number of recaptures in any one sample period caused each of their estimates of the population to be unreliable. One possible cause of this unreliability is that the Jolly–Seber technique uses the number of bears caught both before and after, but not at, period i, and these numbers tend to be extremely small and prone to error. In addition, population estimates could not be derived for the last sample period, thus reducing the value of a sample which was expensive to collect. Finally, Stirling et al. (1975) found that the estimated number of marks in the population at time i, $\hat{M}_i$, was occasionally an impossibly large number. This was either because one of the assumptions of the model was violated or because of random errors associated with small sample sizes. At this time it is impossible to determine which of these two factors is most important.

We derived the population estimate described in this paper as an alternative to current estimation procedures. We do not suggest that any one estimation technique for polar bears will be universally valid, but feel the following method is useful in some situations. One advantage of this technique, relative to the Seber–Jolly estimate, is that it is possible to estimate a population size for the most recent census period.

Methods

The central problem in multiple mark–recapture censuses is to obtain a reliable estimate of the number of marked animals surviving in the population when a recapture is undertaken. The Jolly–Seber method considers M_i in the population at time i to be in two classes: the m_i recaptures at time i, and those not recaptured. If the subsequent sampling is random, on the average the same fraction of marked individuals will be subsequently recaptured whether they were marked and released at time i, or whether they were marks surviving from earlier captures. Equating these expected fractions leads to an estimate of M_i; but it is subject to a sampling error which may be large. The proposed technique, instead, estimates surviving marks each period by directly applying a survival rate to the previous number of marks. A survival rate is derived for the population by aging all captures and fitting a survival curve to the age structure.

The data were collected during a continuing tagging program on polar bears in the western Canadian Arctic from 1970 to 1978 (study area and methods are described in Stirling et al. (1975)).

Estimates of the population were then obtained from the mark–recapture series by:

$$[1] \quad \hat{N}_i = \hat{M}_i/\hat{\rho}_i$$

where $\hat{N}_i$ = estimated population at time i; $\hat{M}_i$ = estimated marks in population before time i; and $\hat{\rho}_i$ = estimated fraction marked before time i; $\hat{\rho}_i$ is given by m_i/n_i where n_i = captures at time i; and m_i = recaptures at time i. $\hat{M}_i$ is estimated by

$$[2] \quad \hat{M}_i = (\hat{M}_{i-1} + R_{i-1} - m_{i-1})\hat{\phi}$$

where R_i = total marks released at time i. $R_i - m_i$ is thus new marks released at time i; and $\hat{M}_i + R_i - m_i$ is the total estimated marks after time i. Survival (ϕ) of these marks to the next capture time gives the estimated marks before that time.

The expected squared error of $\hat{M}_i$ is approximated by:

$$[3] \quad \text{var}\,\hat{M}_i = \sum_{j=1}^{i-1} (R_{i-j} - m_{i-j})\hat{\phi}^j(1 - \hat{\phi}^j) + \left[\sum_{j=1}^{i-1} (R_{i-j} - m_{i-j}) \cdot j\hat{\phi}^{j-1}\right]^2 \text{var}\,\hat{\phi}$$

The first of these terms is the binomial variance due to the random survival of marks. The second is an approximation to that component of error variance of $\hat{M}_i$ which is due to error in the estimation of ϕ (Appendix A).[1] The variance of the population estimate can then be approximated thus:

$$[4] \quad \text{var}\,\hat{N}_i = \text{var}\,\hat{\rho}(\hat{M}_i^2/\hat{\rho}_i^4) + (\text{var}\,\hat{M}_i)/\hat{\rho}_i^2$$

where $\hat{\rho}_i$ and $\hat{M}_i$ are assumed uncorrelated as to error. The variance of $\hat{\rho}_i$ is given by

$$\hat{\rho}_i(1 - \hat{\rho}_i)/(n_i - 1)$$

(The derivation of estimated variances for $\hat{N}_i$ and $\hat{M}_i$ is given in Appendix A.)

The assumptions of this mark–recapture technique can be summarized as follows.

(1) The estimated annual survival rate, $\hat{\phi}$, and its variance, var $\hat{\phi}$, are constant throughout the entire study, are the same for marked and unmarked animals, and are known. Eberhardt (1977) suggests that for most long-lived marine mammals adult survival will be buffered from environmental variation and should remain relatively constant. Stirling et al. (1975) and Lentfer (1974) reported that polar bear populations in the eastern and western Beaufort Sea are distinct from each other with rates of exchange that are probably less than 5% per annum, so that movements in and out of the study area need not be considered. Therefore, changes in rates of annual survival should be solely responsible for changes in the numbers of tagged animals in the population. Survival rates for this population of polar bears were available from data independent of the mark–recapture estimates. All bears handled were aged by the removal and subsequent sectioning of a vestigial premolar (Stirling et al. 1975). An estimate of survival was calculated from the age distribution using an exponential decay curve, fitted by a log-linear regression. Using this method, annual survival (ϕ) was estimated to be 0.88. Comparison of the sex-specific annual survival rates calculated for different populations suggest that they are relatively constant between populations (Lentfer et al. 1977; Stirling et al. 1975). An error variance was deduced by considering a plausible range (0.76–1.0) to be 3.92 (2 × 1.96) standard errors. This gives var $\hat{\phi} = 0.00375$.

(2) Marked and unmarked animals have the same probability of capture. This assumes that marked animals are evenly mixed within the population. This was accomplished in the western Canadian Arctic by spreading the tagging effort as evenly as practical over the study area. The validity of this assumption is enhanced by the annual mixing that occurs when the polar bears in this area move north in early summer because of the retreat of the pack ice (Stirling et al. 1975). In this analysis, we considered all members of the population as independent individuals and

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[1] Appendix A is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

TABLE 1. Data used to estimate polar bear population and subsequent estimates

	i							
	1	2	3	4	5	6	7	8
Year	1970–1971	1971–1972	1972–1973	1973–1974	1974–1975	1975–1976	1976–1977	1977–1978
n_i	32	48	109	109	189	63	36	40
m_i	0	1	4	9	35	13	10	6
R_i	32	46	107	108	187	63	36	38
$\hat{\rho}_i$	—	0.0208	0.0367	0.0826	0.1852	0.2063	0.2778	0.1500
$\hat{M}_i$	—	28.16	64.38	147.29	216.74	324.49	329.55	318.16
SD* $\hat{M}_i$	—	2.69	6.99	16.51	29.69	48.79	65.93	79.85
$\hat{N}_i$	—	1353.85	1754.22	1783.17	1170.30	1572.90	1186.29	2121.07
SD $\hat{N}_i$	—	1346.97	881.65	603.27	239.96	454.98	397.43	959.54
$\hat{M}_i + R_i - m_i$	32	73.16	167.38	246.29	368.74	374.49	355.55	350.16

*Standard deviation.

did not stratify the sample according to age or sex. We did this because stratification would make the sample sizes too small to be useful. Therefore, assumption 2 is not completely met in that marked family groups contain members that are not randomly mixed with the rest of the population. This problem only affects family groups with cubs of the year and yearlings, as most 2 year olds are weaned and become independent shortly after being captured with their mothers. Gilbert (1976) used the Seber–Jolly interval to estimate the number of groups in the population and then used average group size to derive a total population estimate. This has disadvantages in that sample sizes become extremely small and the variance associated with the average group size is difficult to incorporate into the variance estimate for the total population. Future analysis needs to be directed toward identifying how much of a problem this adds to the estimation procedure.

(3) Marked animals do not lose their marks and all marks are reported on recovery. The marking procedure for polar bears involves putting tags on each ear, and tattooing the inside of both upper lips. On recapture, any lost tags are replaced after the animal is reidentified from the lip tattoo. Therefore, tag loss is not thought to be a serious problem. In this analysis, returns of marked animals from Inuk hunters were not incorporated because of the biases introduced by only having marked animals reported, instead of the total kill. Therefore, problems associated with not identifying or misidentifying marked animals from hunter returns were avoided.

(4) All samples are instantaneous. Instantaneous in this sense is relative to the survival of the population members (Siniff et al. 1977). For polar bears, annual survival is high enough to make mortality negligible between the start and the end of each sampling period.

Results

The estimates of population size (Table 1) suggest that the numbers of polar bears in the western Canadian Arctic declined markedly between the springs of 1974 and 1975, as previously reported by Stirling et al. (1975). Several independent sources of data support this suggestion. Between 1974 and 1975, the numbers of ringed seals dropped by 50% (Stirling et al. 1977) and their productivity by 90% (Smith and Stirling 1975, 1976). The natality rates of polar bears and the numbers of females accompanied by cubs of any age dropped by about 50 and 35% respectively between 1971–1973 and 1974–1975 (Stirling 1978). Finally, subadult male and female polar bears weighed significantly less in 1974 and 1975 than in 1971–1973 (Kingsley 1979). The environmental changes that began in the winter of 1973–1974 affected seal numbers and reproduction in the spring of 1974. Although the effects of the changes in seal distribution and abundance began to affect the survival of young bears and their weights immediately, the 1974 polar bear population estimate was taken too early in the year to detect the reduction in numbers that was so apparent by 1975.

Following the decline in numbers of both ringed seals and polar bears, the population of polar bears was expected to remain low for a period or to show, a gradual increase as seal numbers recovered. Aerial surveys of the distribution and abundance of ringed seals in 1976 and 1977 replicated the surveys of 1974 and 1975 but showed no increase in the population (Stirling, personal communication). However, the estimates of the polar bear population from 1976 through 1978 were erratic and their variances were sufficiently large that significant differences could not be established.

It is critical to evaluate why the technique was sufficiently sensitive to pinpoint the decline in 1974–1975 so accurately but gave inconsistent results in the subsequent 3 years. On inspection, it appears related to sample size. The samples in the 3 years leading up to 1974–1975 all exceeded 100 animals while those in the following 3 years were all much smaller. Another explanation is that ρ_i was inappropriately estimated because of problems in obtaining a representative sample. It is known that females with cubs of the year are underrepresented in the sample of captured bears (Stirling et al. 1975). It is also known that recaptures of family groups produce an upward bias in the estimation of ρ_i. In the light of the small sample sizes, this type of

TABLE 2. (*a*)$(R-m)\hat{\phi}^j(1-\hat{\phi}^j)$ and the sum of such terms*; (*b*)$j\hat{\phi}^{j-1}(R-m)$ and the sum of such terms; and (*c*) data used to estimate variance of polar bear population estimate, and subsequent estimates

	i							
	1 (1970–1971)	2 (1971–1972)	3 (1972–1973)	4 (1973–1974)	5 (1974–1975)	6 (1975–1976)	7 (1976–1977)	8 (1977–1978)
	(*a*) $(R-m)\hat{\phi}^j(1-\hat{\phi}^j)$ and the sum of such terms							
	(32)	3.38	5.59	6.95	7.68	7.98	7.96	7.73
		(45)	4.75	7.86	9.77	10.80	11.22	11.19
			(103)	10.88	17.99	22.36	24.73	25.67
				(99)	10.45	17.30	21.49	23.77
					(152)	16.05	26.56	32.99
						(50)	5.28	8.74
							(26)	2.75
$\sum_j(R-m)\phi^j(1-\phi^j)$†		3.38	10.34	25.69	45.89	74.49	97.24	112.84
	(*b*) $j\hat{\phi}^{j-1}(R-m)$ and the sum of such terms							
	(32)	32.00	56.32	74.34	87.23	95.95	101.32	104.03
		(45)	45.00	79.20	104.54	122.66	134.93	142.49
			(103)	103.00	181.28	239.29	280.77	308.84
				(99)	99.00	174.24	230.00	269.86
					(152)	152.00	267.52	353.13
						(50)	50.00	88.00
							(26)	26.00
$\sum_j j\phi^{j-1}(R-m)$		32.00	101.32	256.54	472.05	784.14	1064.54	1292.35
$(\sum_j j\phi^{j-1}(R-m))^2$ var ϕ‡		3.84	38.50	246.80	835.62	2305.78	4249.67	6263.13
var $\hat{M}$		7.22	48.84	272.49	881.51	2380.27	4346.91	6375.97
	(*c*) Data used to estimate variance of polar bear population estimate, and subsequent estimates							
var $\hat{M}_i$	—	7.22	48.84	272.49	881.51	2 380.27	4 346.91	6 375.97
$(1/\hat{\rho}_i^2)$ var $\hat{M}_i$	—	16 688.24	36 261.31	39 938.38	25 700.72	55 927.80	56 326.94	283 376.44
$(\hat{M}_i^2/\hat{\rho}_i^4)$ var $\hat{\rho}_i$	—	1 797 651.34	741 035.16	323 995.23	31 881.92	151 084.80	101 625.08	637 347.54
var $\hat{N}_i$	—	1 814 340	777 300	363 930	57 580	207 010	157 950	920 720
Percentage of var $\hat{N}_i$ associated with $(1/\hat{\rho}_i^2)$ var $\hat{M}_i$	—	0.92	4.67	10.97	44.63	27.02	35.66	30.78

*Entries in parentheses are $(R_i - m_i)$. Succeeding entries on the same line are $(R_i - M_i)\phi^j(1-\phi^j)$ for successive values of j.
†ϕ = 0.88.
‡var ϕ = 0.00357.

problem could be responsible for the erratic estimate of population size.

In an effort to reduce the variance associated with the estimated population, an analysis of the relative contribution to the total variation of various components of the variance estimate was conducted (Table 2). The fraction of the total variation of $\hat{N}_i$ that was associated with the term $(1/\hat{\rho}_i^2)$ var $\hat{M}_i$ ranged between 0.01 and 0.45. Thus most of the error variance of $\hat{N}_i$ was contributed by the term $(\hat{M}_i^2/\hat{\rho}_i^4)$ var $\hat{\rho}_i$. Noting that

$$[5]\quad \hat{M}_i = \hat{\rho}_i\hat{N}_i$$

the var $\hat{N}_i$, when rewritten to incorporate Eq. 5, becomes

$$[6]\quad \mathrm{var}\,\hat{N}_i = (\hat{N}_i^2\,\mathrm{var}\,\hat{\rho}_i + \mathrm{var}\,\hat{M}_i)/\hat{\rho}^2,$$

with the term $\hat{N}_i^2$ var $\hat{\rho}_i$ predominating. Assuming that var $\hat{N}_i$ is negligible compared with $\hat{N}_i^2$ var $\hat{\rho}_i$, Eq. 6 can be rewritten as

$$[7]\quad \mathrm{var}\,\hat{N}_i = [\hat{N}_i^2(1-\hat{\rho}_i)]/[(n_i-1)\hat{\rho}_i]$$

Equation 7 is useful in predicting the standard error of an estimated $\hat{N}_i$ for a particular sample size. Assuming that $\hat{N}_i$ equals 1500 and $\hat{\rho}_i$ equals either 0.1 or 0.2, the precision of the estimate for N_i increases very rapidly as sample sizes initially increase (Fig. 1). However, the precision of the estimate does not increase as rapidly after sample size reaches 200. This analysis suggests that with the population estimation technique described in this paper, relatively imprecise estimates will be produced with sample sizes of less than 50, given that the proportion of marked animals in the population is between 0.1 and 0.2. Sample sizes of 150 will produce a much more precise estimate, but the cost of such a sample may be prohibitive. If research needs demand a particular level of confidence, cost needs to be taken into consideration. However, samples of less than 50 should probably be discouraged regardless and sample sizes of 150 or more should be encouraged if possible.

The analysis of the various sources of variance (Table 2) also shows a progressive increase in var

TABLE 3. Comparison of population estimates from Lincoln–Peterson and Seber–Jolly models

	i							
	1 (1970–1971)	2 (1971–1972)	3 (1972–1973)	4 (1973–1974)	5 (1974–1975)	6 (1975–1976)	7 (1976–1977)	8 (1977–1978)
	Lincoln–Peterson estimates							
M_i	0	32	77	180	279	431	481	507
$\hat{N}_i$	—	1538	2098	2179	1506	2089	1731	3380
	Seber–Jolly estimates							
r_i	8	17	16	26	11	0	0	—
z_i	0	7	20	27	18	16	6	0
$\hat{M}_i$	0	20	138*	121	341*	—	—	—
$\hat{\rho}_i$	0	0.0208	0.0367	0.0826	0.1852	0.2063	0.2778	0.1500
$\hat{N}_i$	—	962	3760	1465	1841	—	—	—
$\hat{\phi}_i$	0.62	2.12	0.50	1.55	—	—	—	—

*M_i is larger than maximum M_i possible.

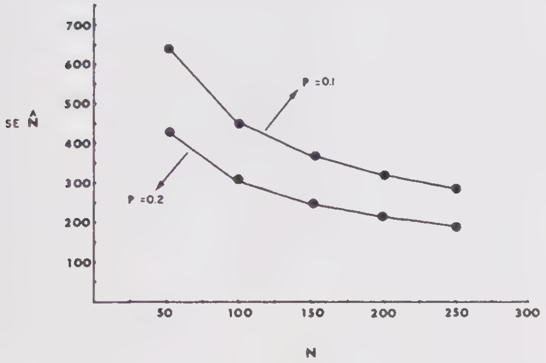

FIG. 1. Sample size versus standard error of population estimate. ρ, proportion of population that is marked; n, sample size; SE $\hat{N}$, standard deviation of the population estimate.

$\hat{M}_i$. The components of variation due to var $\hat{M}_i$ form an increasing fraction of the error variance of $\hat{N}$, and this suggests that this estimation procedure will have to be truncated when this source of variation starts to predominate in the error variances of $\hat{N}_i$. Presumably, this could be avoided if a Seber–Jolly estimate of $\hat{M}_i$ could be made at some point during the study. However, so far, the principal contribution to the error of $\hat{N}_i$ is associated with the var $\hat{\rho}_i$. Therefore, the most effective way of increasing the precision of the estimate of N_i is to increase the proportion of marked animals in the population or to increase the number of animals that are captured in each sample period.

Discussion

The crux of this technique is the incorporation of additional independent information in the estimation of the number of marks in the population at time i. In this case, survival estimates allow for the estimation of M_i in an open population. The survival rate is estimated from age structure data and necessarily assumes that (1) the growth rate of the population is incorporated into the survival estimate (Payne 1977), (2) the survival rate is constant, and (3) the age structure of the population is stationary. The estimation of M_i also assumes that emigration of marked animals is negligible or at least absorbed in the survival estimate. One advantage with incorporating additional information into the population model is that the model need not be as general and can therefore be more efficient in estimating specific parameters of the population.

A comparison of Lincoln–Peterson and Seber–Jolly population estimates (Table 3) with the estimates produced in this paper suggests that assumptions of the Lincoln–Peterson and Seber–Jolly models are unavoidably violated. The closed population assumption of the Lincoln–Peterson model produces an estimated number of marks that is necessarily biasing $\hat{N}_i$ upwards. This is because the estimated number of marks in the population ($\hat{M}$) at time i assumes that none of the animals previously marked have suffered any mortality. Therefore, $\hat{M}_i/\hat{\rho}_i$ will tend to be too large.

The Seber–Jolly estimates (Table 3) are known to be unreliable because two of the four estimates of $\hat{M}_i$ are larger than the maximum number of marks that could exist. This is reflected in survival rates that are greater than 1.0 for these 2 years. Specifically which assumption of the Seber–Jolly model is violated is not clear. Sample sizes in specific years may be responsible for overestimating M_i. It may also be that r_i/R_i may not equal $Z_i/(\hat{M}_i - m_i)$ (this is necessarily assumed with Seber–Jolly estimate of $\hat{M}_i$: see Seber 1973, p. 196). However, the reasons why these two ratios would not be equal have not been identified as yet.

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Tetracycline Marking and the Possible Layering Rate of Bone in an Amazonian Manatee *(Trichechus inunguis)*[1]

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ABSTRACT

This paper reports the first successful use of tetracycline marking of layered bone in a manatee and suggests that this technique may be useful in estimating age for species of this family. A six-month-old male Amazonian manatee *(Trichechus inunguis)* was first injected with *Terramycin* on 23 August 1976 (2.2 mg/kg) and subsequently on 18 and 19 November 1977 (7.1 and 8.5 mg/kg, respectively). After the animal died, on 3 May 1978, a transverse thin section of one of its ribs was examined microscopically using plain and polarized transmitted light and ultraviolet reflected light. One fluorescent mark, probably representing the 1977 injections, was found in the periosteal bone between the first and second of three layers containing aligned Haversian systems. It is likely that, for this species, 2.2 mg/kg dosages are insufficient to mark bone, but dosages between 7.1 and 8.5 mg/kg are adequate. An average accumulation rate of one layer per year is suggested by our analysis of this specimen.

INTRODUCTION

In recent years the use of hard-tissue layering systems to determine age has become an important area of research in biological studies on sirenians. For dugongs the problem is simplified by the presence in these animals of tusk-like incisors that contain well-defined dentinal growth layer groups (Scheffer, 1970; Mitchell, 1976, 1978; Kasuya and Nishiwaki, 1978; Marsh, this volume). The manatees possess no incisors; their molariform teeth are rapidly and continuously replaced and growth layers do not accumulate (Odell, 1977). Age estimates for manatees have been based on body lengths (loc. cit.).

Since the histological study by Fawcett (1942) it has been known that certain bones of the manatee contain growth layers. His descriptive comments foreshadow the use of bone growth layers to determine age in manatees:

> The arrangement of periosteal bone [in the ribs of manatees], distinguished by slight differences of internal architecture, suggest that the osteogenic activity of the periosteum is periodic or seasonal. . . the most recently deposited bone is found. . .[on the outer curvature of the rib]. . . while older and older layers are encountered toward the inner edge. (p. 277)

Odell (1977) was unable to define growth lines in prepared histological sections of the manatee ribs that he examined. No other attempts at age estimation of manatees using growth layers have been reported.

Layering rates in hard tissues of sirenians are not known due to a lack of animals of known age (Marsh, this volume; Odell, 1977). Marsh (this volume) reports that

> There have been no successful field studies of specific individuals [of dugongs] over any time span. . . [and although they] have rarely been maintained in captivity [they] have never been bred in captivity.

Several manatees have been born in captivity (Odell, 1977). Apparently, none of these has been examined for growth layers.

Layering rates in marine mammals may be studied by use of *in vivo* administrations of tetracycline antibiotics which are incorporated into the hard tissue shortly after their introduction (Yagi, Nishiwaki and Nakajima, 1963; Best, 1976; Gurevich, Stewart and Cornell, this volume; Myrick, this volume). If given in dosages of sufficient strength, tetracycline labels the layer which is forming at the time the drug is introduced. The label may later be identified as a fluorescent band in the tissue when thin sections are viewed microscopically with reflected ultraviolet light.

The *average* layering rate may be calculated by dividing the number of layers that have accumulated since the marking event by the time elapsed between marking and death of the animal. By assuming that the layering rate is constant, one may estimate the animal's age by counting all layers and multiplying that value by the depositional rate.

This paper reports the first successful tetracycline-marking of skeletal tissues in an Amazonian manatee, indicates the adequate dosage required to produce a detectable mark in the tissues, and suggests the layering rate of periosteal bone. This technique should be of value in future studies of age and growth of sirenians.

MATERIALS AND METHODS

A male *Trichechus inunguis* calf, probably less than six months old and in severely malnourished condition (total curved-line length 93 cm, weight 9.1 kg), was given a single intramuscular injection of 20 mg of *Terramycin* (a tetracycline antibiotic) (dosage 2.2 mg/kg) on 23 August 1976. It was maintained thereafter on a diet of milk formula and aquatic plants. By 16 November 1977 it had reached a curved-line length of 125 cm and a weight of 35.2 kg. Single intramuscular injections of 250 and 300 mg of *Terramycin* were given on 18 and 19 November, respectively (dosages 7.1 and 8.5 mg/kg). The animal died on 3 May 1978, at a length of about 128 cm and still weighing about 35 kg; the lack of further growth was attributed to termination of the milk diet. The frozen carcass of the animal used in this study is preserved at the Instituto Nacional de Pesquisas da Amazônia (INPA), Departamento Peixe-Boi, Manaus, Brazil (catalog number INPA-PB 11).

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[1] Contribution No. 21 from the Department of Aquatic Mammal Biology, INPA, Manaus, Brazil.
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A left rib from the middle thorax (chord length 15.5 cm) was cleaned by maceration and cut transversely at the midpoint of its length, and a thin section (anteroposterior diameter 15 mm, mediolateral diameter 10 mm, thickness ≅ 75 μm) was cut with a diamond saw (Fig. 1). The section was mounted in *Permount* and viewed at 50 to 200 X in reflected ultraviolet light, using a *Zeiss* fluorescent vertical illuminator with a filter reflector No. 48-77-05 combination and in plain and polarized transmitted light. Plain and polarized transmitted-light examinations of several thin sections taken from ribs and mandibles of adult and young adult manatees from Florida were made for histological comparison.

RESULTS

Histology

The histological arrangement of the bone in the thin section examined by one of us (Myrick) corresponds to that described by Fawcett (1942) for thin sections of manatee ribs. The section consists of a stratified series of concentric zones of densified bone that arch outwards from the pleural edge. According to Fawcett (1942) these zones result from different proportions and arrangements of primary (fetal) trabeculae that have become filled gradually by secondary bone, forming a dense central core. They are invested by abundant nutritive channels, but contain progressively fewer Haversian systems toward the outer curvature.

Toward the outer curvature of the section the original fetal trabecular architecture of primary spongiosum is easily recognizable (see Figs. 1 and 2); the inter-trabecular spaces are large and the walls have not been thickened appreciably by deposition of secondary bone. The more proximal trabeculae are thickened, with spaces that are

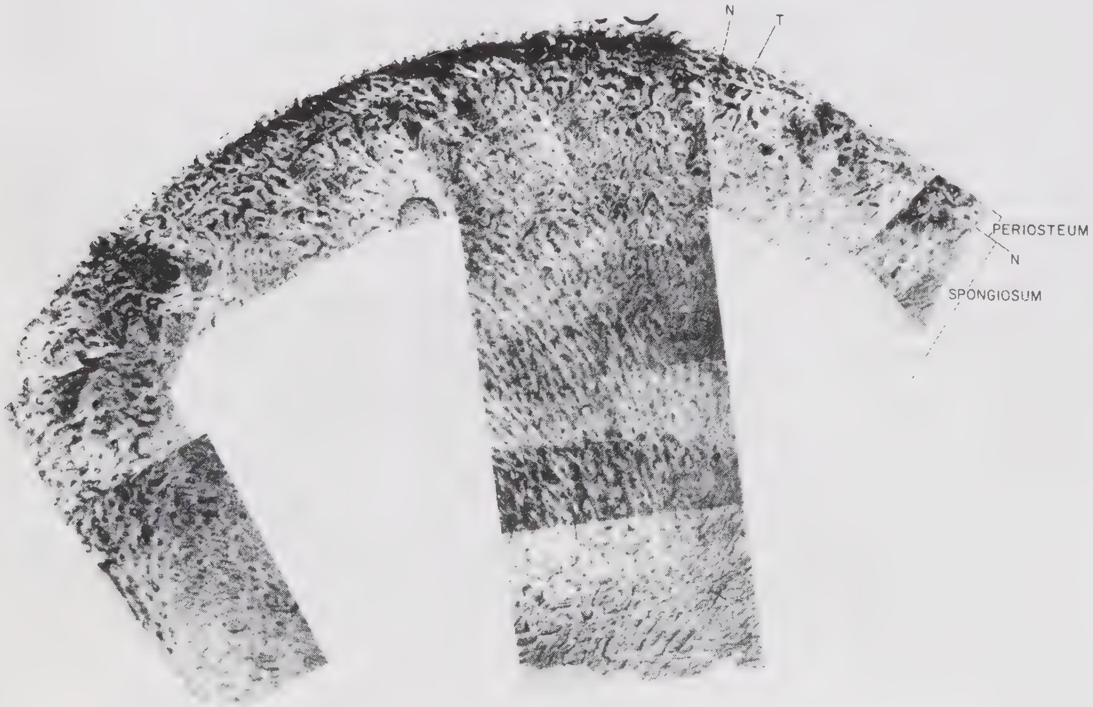

Fig. 1. Composite photograph of transverse thin section of rib from 2.2 year old male *Trichechus inunguis*, viewed in low-contrast crossed polarized light (×12). Abbreviations: N = probable location of neonatal line separating periosteal bone from spongiosum. T = approximate level of periosteal tissue in which fluorescent mark from *Terramycin* injection may be seen under ultraviolet light.

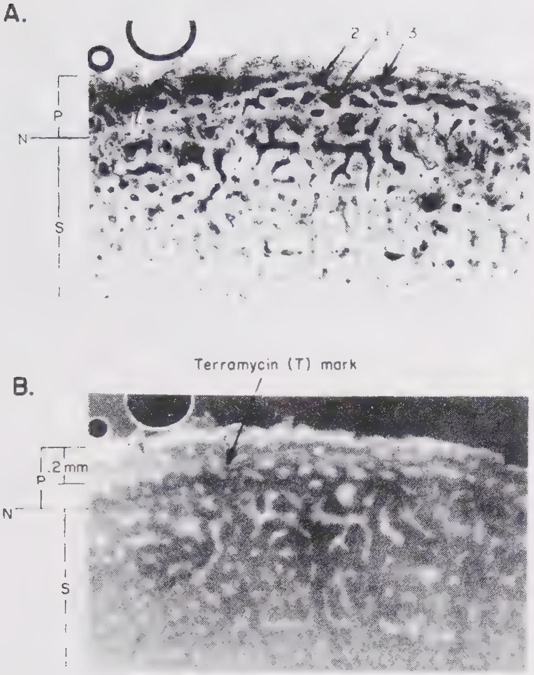

Fig. 2. Transverse thin section of rib as shown in Fig. 1, showing histology near the external margin (×50).

A. Low-contrast polarized light photograph showing three layers (numbered) of aligned Haversian systems in periosteal bone (P). N indicates neonatal line separating periosteal bone from spongiosum (S).

B. Section as shown in A using reflected ultraviolet light. *Terramycin* (T) is represented by fluorescent band (arrow). N indicates well-defined dark region representing neonatal line.

almost entirely filled. Apparently, the deposition of secondary bone commences in the pleural region and progresses outwardly toward the external surface (Fawcett, 1942).

The boundary between the periosteal bone and the fetal core of primary spongiosum is recognized by a sharp change in orientation and shape of the trabeculae. The trabeculae of the core tend to be columnar and radiate outwards from the pleural region in an irregular pattern. The neonatal boundary, i.e. where deposition of periosteal bone begins, truncates the fetal trabeculae with a thickened, continuous envelope of bone containing abundant, flattened osteocytes whose long axes lie parallel to the external curvature of the rib.

External to the neonatal boundary, the bone contains two, possibly three layers of Haversian systems that tend to be open and flattened somewhat, with long axes that are arranged end-to-end, parallel to the external curvature. The bone surrounding the Haversian systems forms a series of more or less continuous walls that accentuate the stratified pattern, but no cemental (adhesion) lines, as described in Fawcett's study, were found in the periosteal bone in the section.

Structures marked by tetracycline

Ultraviolet light produced fluorescence as follows (see Figs. 2 and 3).

(1) Fluorescent rings in the walls of open trabeculae internal to the periosteal (i.e. neonatal) boundary.

(2) Fluorescent rings in the walls and fluorescence of the canaliculi of the Haversian systems comprising the first and second layers, but not the third layer (Figs. 3A, B).

(3) A single, continuous, somewhat irregular fluorescent band situated between the first and second layers of Haversian systems, most closely associated with the second layer, approximately 0.2 mm internal to and parallel with the outer curvature of the bone (Figs. 2B, 3B).

DISCUSSION

Osteogenic activity indicated by fluorescent labels

(1) ***Deposition of secondary bone*** – As indicated by the fluorescent labels, the peripheral systems immediately internal to the periosteal boundary were active when the bone was labelled. This agrees with the interpretation (Fawcett, 1942) that the inter-trabecular spaces of the fetal spongiosum become filled with secondary bone after the fetal framework is formed.

(2) ***Activity and deposition of periosteal bone*** – Fluorescence in the walls and canaliculi of the Haversian systems in the first and second layers indicate that osteoblastic systems in both layers were active at the time tetracycline was introduced. Intimate association of the fluorescent band with the Haversian systems of the second layer suggests that this layer was forming at the time the bone was being labelled. The absence of fluorescence in Haversian systems comprising the third, outermost layer shows that this layer was formed after the tetracycline was incorporated into the system.

(3) ***Adequate dosage required to label bone*** – Three *in vivo* injections of *Terramycin* were given; one (2.2 mg/kg) on 23 August 1976 and the others (7.1 and 8.5 mg/kg) on 18 and 19 November 1977, respectively. Because only one fluorescent band was visible in the section and the 1977 dosages were stronger, we interpret the 18–19 November administration dates to be represented by the band. Apparently, the injection given in 1976 was of inadequate strength to produce a visible mark. We conclude that a dosage of between 7.1 and 8.5 mg/kg is sufficient to label the bone.

(4) ***Possible layering rate in periosteal bone*** – If, as we presume, the animal was (at most) six months old when the first injection was given (August 1976), it would have been about 2.2 years old when it died in May 1978. The total thickness of periosteal bone, containing two and part of a third layers of Haversian systems, would then represent 2.2 years of accumulation. Division of layers by that elapsed time gives an *average* layering rate of approximately one layer per year for the specimen (see Figs. 3B, 3C). However, the animal was young and in poor health and the layers in its rib used in the calculation of layering rate are not separated by adhesion lines observed in peripheral periosteal layers in ribs of adults. No ontogenetic series of rib sections of young and mature animals was available for detailed histological comparison of the early layers. This precludes a confident blanket statement regarding layering rates in periosteal bone of manatees in general.

(5) ***Periosteal layers in other specimens***

Ribs – Haversian systems were not discernible in large numbers in thin sections of periosteal bone from other

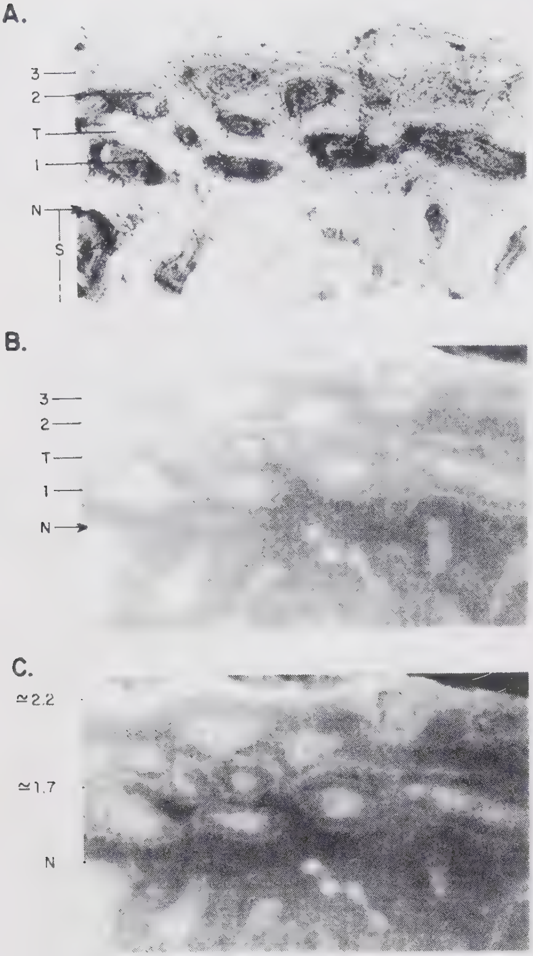

Fig. 3.A. Highly magnified (×200) view in low-contrast polarized light of section shown in Fig. 2. Two and part of a third layer(s) of aligned Haversian systems are shown (numbered).
B. Section as in A viewed with reflected ultraviolet light showing fluorescent labels ringing Haversian systems in layers one and two but not in those of the third. Brightness at external margin (top) is autofluorescence which is not of same quality or colour as that produced by the *Terramycin*. (See Fig. 2 for abbreviations.)
C. Section as in B showing time brackets applied to layers used to obtain estimate of layering rates. N indicates time of birth. ≃1.7 indicates accumulation after 1.7 years when the second and third injections of *Terramycin* were administered. ≃2.2 indicates approximate age in years when animal died.

specimens *(T. manatus)* examined by one of us (Myrick). In these specimens the layers contained only flattened osteocytes aligned parallel to the bones' external curvatures. Nevertheless, the boundary (earliest) layer in each section truncated the columnar arrangement of the spongiosum as was observed in the section of marked manatee rib. An ontogenetic series of ribs from neonates through young adults (not available to us) might help in determining whether or not the presence of Haversian systems in the boundary layers is characteristic of the formation of early periosteal bone in manatees. It would also be useful in defining the absorption rate (if any) of periosteal layers in adult specimens.

Mandibles – Although layers were fairly well definable in some of the rib sections examined, they do not always occur with equal clarity or in adjacent areas of the same rib (see Fawcett, 1942; Marsh, this volume). On the other hand, transverse thin sections taken from the posterior regions of mandibular rami of two Florida manatees were found (by Myrick) to show layering very clearly and continuously. These layers appear to be more easily distinguishable than the periosteal layers in ribs. Odell (1977) suggested that investigation of the layers in flipper bones of the manatee might prove useful in making age estimates, but we now believe that periosteal layering in the mandible will give superior results (see also Mitchell, 1978).

SUMMARY

The study suggests the following:

(1) Tetracycline antibiotics may be used safely to label periosteal bone of manatees.

(2) The dosage sufficient to produce a detectable mark under ultraviolet light is between 7.1 and 8.5 mg/kg of body weight.

(3) Periosteal bone may be deposited at a rate of one layer per year in manatees, but data are inconclusive.

(4) In the rib of the manatee, the boundary (i.e. neonatal line) between the fetal spongiosum and the periosteal (postnatal) compactum is demarcated by a truncation of the columnar trabeculae by tissues arranged parallel to the external curvature of the bone.

We make the following recommendations:

(1) Age determination studies of manatees should include investigations of the layering patterns of periosteal bone in the posterior region of the mandible which seems to be superior to ribs in discernibility of layers.

(2) When possible, future studies should include construction of an ontogenetic series of bone samples ordered by carcass body length and separated by sex. Samples would provide information on relative age, ontogenetic development of layers, and deposition and resorption patterns.

(3) When feasible, live animals should be sexed, measured, tagged, and injected with tetracycline in anticipation of future recovery of their carcasses.

ACKNOWLEDGEMENTS

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D'VINCENT ET AL.: LARVAE AND EARLY JUVENILES OF PACIFIC BUTTERFISH
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DESCRIPTION OF THE LARVAE AND EARLY JUVENILES OF THE PACIFIC BUTTERFISH, *PEPRILUS SIMILLIMUS* (FAMILY STROMATEIDAE)

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ABSTRACT

Larvae of the stromateid fish, *Peprilus simillimus*, are relatively common in nearshore samples of California Cooperative Oceanic Fisheries Investigation (CalCOFI) plankton samples taken off central California to Baja California. This paper describes the larvae of *P. simillimus* from hatching to juvenile and presents criteria for distinguishing early-stage larvae of this species from those of similar-appearing species, in particular the white croaker, *Genyonemus lineatus*. Analysis of *P. simillimus* larvae from CalCOFI survey cruises of 1975 showed a near-coast distribution with areas of concentration in the Southern California Bight and Bahia Sebastian Viscaino, where the shelf is relatively broad.

RESUMEN

Las larvas de *Peprilus simillimus* son bastante comunes en las muestras de plancton colectadas en la zona nerítica durante el programa CalCOFI (California Cooperative Oceanic Fisheries Investigations), desde California central hasta Baja California. En este trabajo se describen las fases larvales de *P. simillimus*, desde su eclosión del huevo hasta la fase juvenil, y se presentan los criterios básicos para distinguir los primeros estados larvales de esta especie y de otras especies similares, en particular *Genyonemus lineatus* (roncador blanco). Las larvas de *P. simillimus* colectadas durante los cruceros de CalCOFI en 1975, presentaron una distribución nerítica, y se concentraron principalmente en la Bahía del Sur de California y la Bahía Sebastián Vizcaíno, donde la plataforma continental es más ancha que en el resto del litoral.

INTRODUCTION

The stromateid fish, *Peprilus simillimus,* is one of four eastern Pacific species of *Peprilus* and is the only one found north of Mexico (Horn 1970). It ranges from Bahia Magdalena, Baja California (ca. 24°N), north to British Columbia (ca. 55°N; Miller and Lea 1972). Marketed as Pacific butterfish or Pacific pompano, it is the subject of a minor fishery with a recent peak of 182,000 pounds in 1971 (Oliphant 1973).

Juveniles and adults of *P. simillimus* are found associated with nearshore soft-bottom habitats, and the larvae occur in coastal CalCOFI stations from Point Conception, California, to Bahia Magdalena, Baja California (Horn 1970).

The early larval stages of *P. simillimus* can be confused with those of some other species, particularly the white croaker, *Genyonemus lineatus*. The purpose of this paper is to describe the development of *P. simillimus* from hatching to juvenile, to provide criteria for distinguishing the early larval stages from those of similar-appearing species, and to summarize the distribution of the larvae in CalCOFI samples from 1975.

METHODS AND MATERIALS

A life history series was assembled consisting of newly hatched larvae to fully transformed juveniles. Most of the larvae were obtained from the CalCOFI ichthyoplankton collections. Other larval and juvenile material was obtained from Scripps Institution of Oceanography (Food Chain Research Group), SIO Fish Collection, and the Los Angeles County Museum. A few specimens were reared incidentally with other species at the Southwest Fisheries Center, La Jolla.

A series was established for the study of morphological development, morphometrics and pigment formation, using the techniques and terminology of Ahlstrom et al. (1976). A second series was cleared in KOH-glycerine and stained with Alizarin Red-S to study the development of meristic characters.

Terminology of specimen length follows that described in Moser and Ahlstrom (1978). Standard length is defined as the distance between the tip of the snout and the posterior edge of the hypural plate. In larvae that have not completed notochord flexion, that is, before the edge of the hypural plate becomes vertical, the body length is measured from the snout to the tip of the notochord.

DESCRIPTION

Literature

Larvae of two Atlantic species have been described, *P. paru* by Pearson (1941) and *P. triacanthus* by several workers (summarized in Martin and Drewry 1978).

Distinguishing Features

P. simillimus hatch at 1.8-2.0 mm, undergo notochord flexion at about 4.8-6.2 mm, and begin to transform into juveniles at about 20 mm. Our smallest fully transformed juvenile is 27.9 mm.

Yolk-sac larvae have scattered melanophores along

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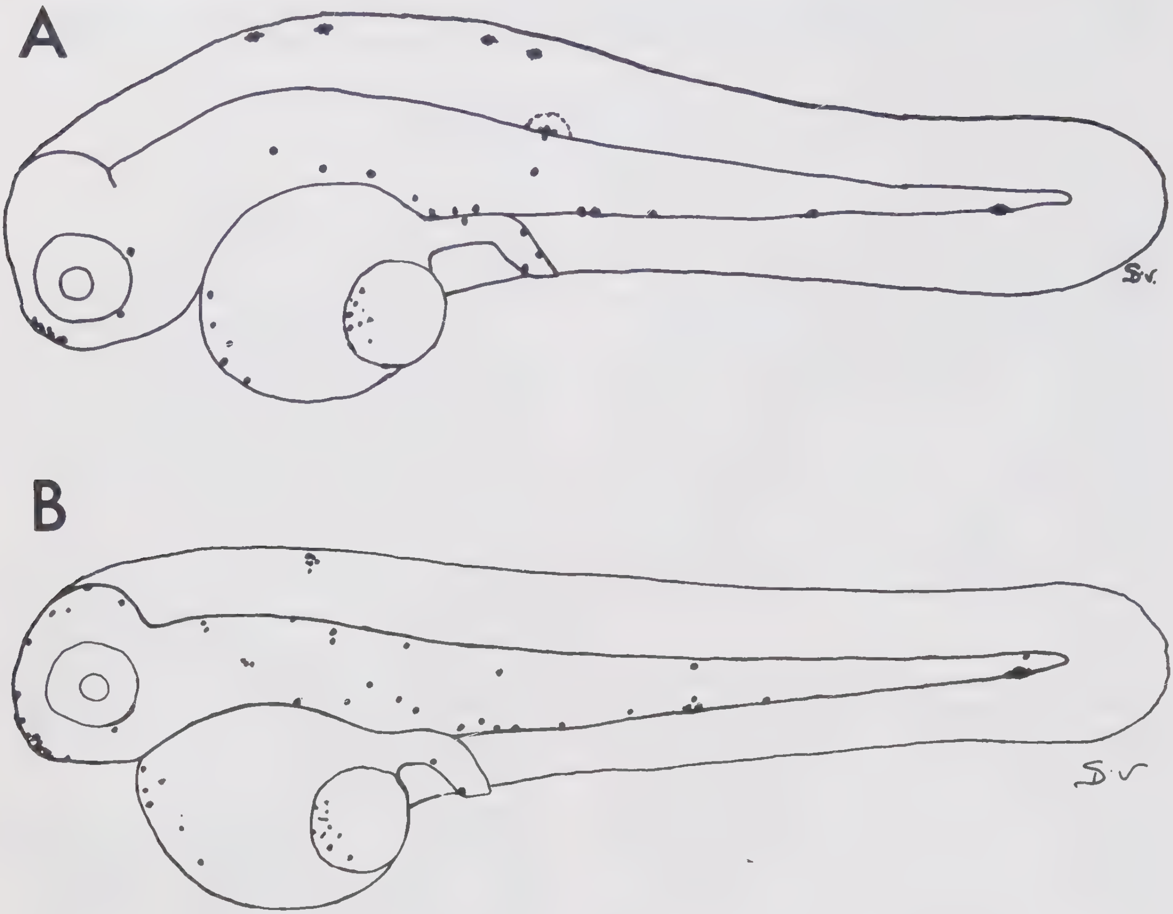

Figure 1. Yolk-sac larvae of A. *Peprilus simillimus* (2.0 mm) and B. the white croaker, *Genyonemus lineatus* (2.1 mm).

the ventral region of the head and body and are characterized by a prominent median dorsal melanophore located slightly posterior to a vertical from the anus. This serves to distinguish them from the yolk-sac larvae of the white croaker, *G. lineatus*, which lack pigment in this area (Figure 1). At the completion of yolk absorption, the larvae have a prominent zone of large melanophores on the trunk above the gut and a median ventral series extending from the cleithrum to the anus (Figure 2). The latter series helps to distinguish early larvae of *P. simillimus* from those of the spotted turbot, *Pleuronichthys ritteri*, which lack the median ventral series. In larger *P. simillimus* larvae, the deep head and body form, and the lateral zone of large melanophores, which gradually expands to cover the entire body, are distinguishing features (Figure 3).

Morphology

Newly hatched larvae have a robust body form, a sizable yolk-sac with a posteriorly located oil globule (ca. 0.2-mm diameter), a moderately long gut (snout to anus distance/body length = ca. 0.50 mm), an incomplete mouth, and unpigmented eyes. At a length of 2.2 mm the yolk is absorbed, the mouth is formed, the eyes are becoming pigmented, and the gut is beginning to coil. Notochord flexion occurs in the larval length range of 5.0-7.0 mm (Table 1). Morphometric proportions are summarized in Table 2. The most conspicuous trend is the two-fold increase in relative body depth during ontogenesis. Other more subtle ontogenetic trends are a relative shortening of snout-to-anus length, an increase in relative head length, and a decrease in relative eye size.

Small spines develop on the preopercular margin.

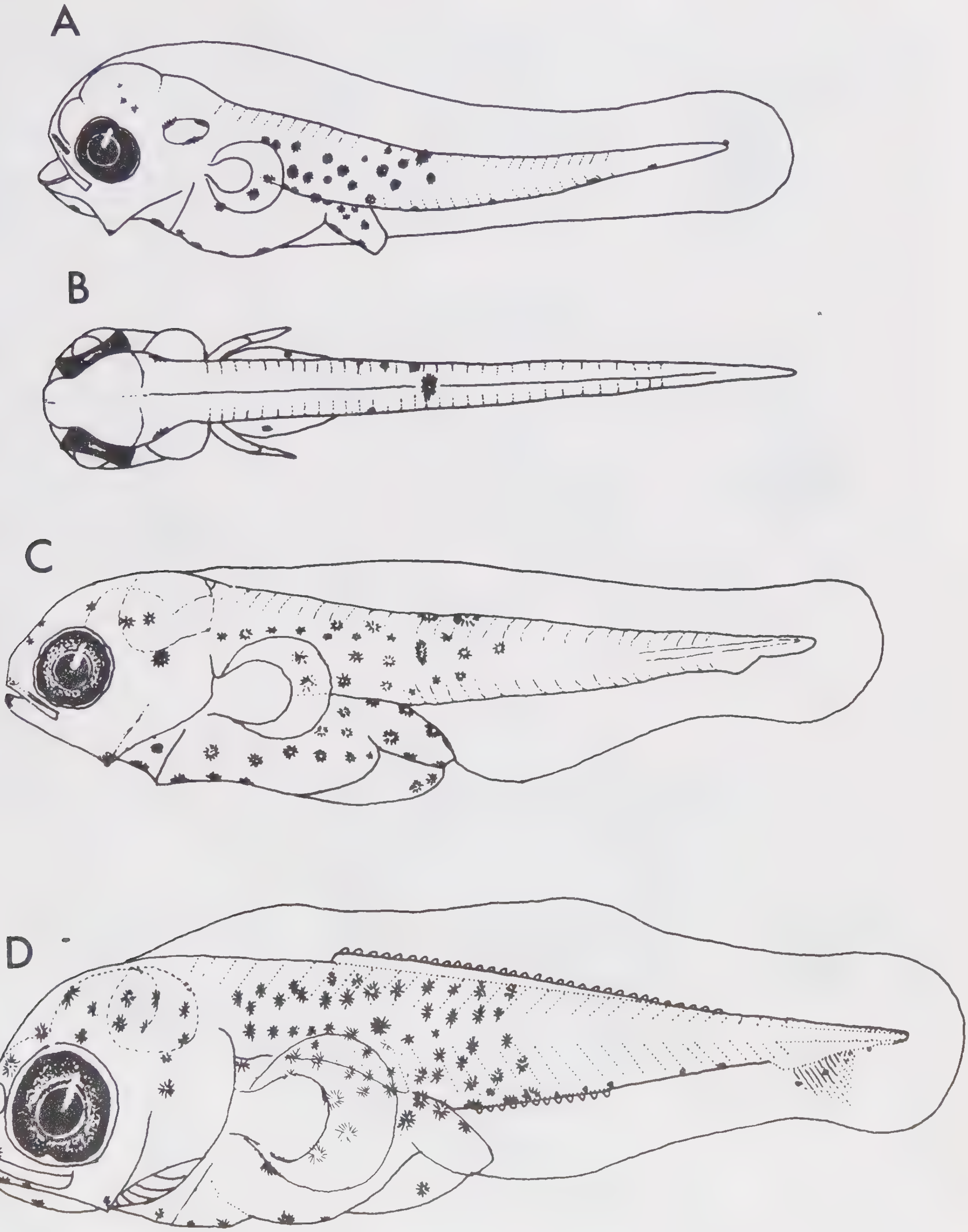

Figure 2. Developmental stages of *Peprilus simillimus*: A) 2.4 mm; B) 2.4 mm, dorsal view; C) 4.1 mm; D) 4.7 mm.

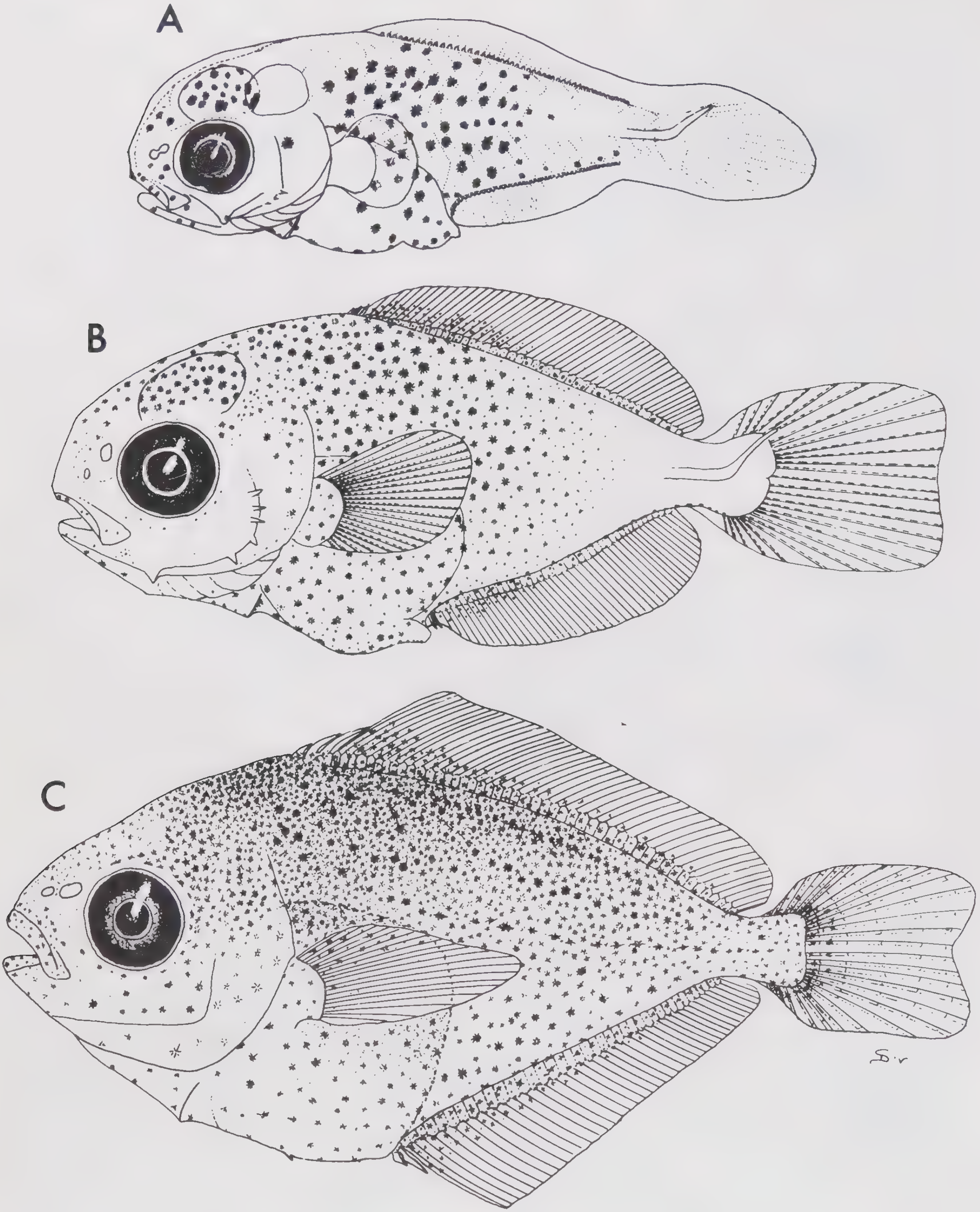

Figure 3. Developmental stages of *Peprilus simillimus*: A) 6.5 mm; B) 10.8 mm; C) transforming specimen, 21.3 mm.

TABLE 1

Measurements in mm of Developmental Series of *Peprilus simillimus*.[1]

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to dorsal fin origin	Snout to anal fin origin	Snout to pelvic fin origin
7505-120.26	1.9	1.0	0.27	0.18	0.08	0.48	–	–	–
7505-120.26	2.3	1.1	0.39	0.22	0.12	0.52	–	–	–
7505-120.24	2.6	1.4	0.54	0.23	0.12	0.58	–	–	–
7803-90.27.6	3.3	1.9	0.83	0.36	0.16	0.98	–	–	–
7803-90.27.6	3.9	2.2	0.98	0.40	0.18	1.1	–	–	–
7803-87.36	4.2	2.5	1.0	0.44	0.23	1.4	–	–	–
7510-120.25	4.8	2.6	1.3	0.49	0.31	1.4	–	2.5	–
6204-130.30	5.4	3.0	1.5	0.56	0.29	1.5	–	2.9	–
6902-127.34	5.5	3.0	1.5	0.56	0.35	1.6	–	3.0	–
7803-93.29	5.8	3.3	1.7	0.64	0.39	1.8	–	3.2	–
7511-83.44.7	6.0	3.2	1.7	0.64	0.39	1.8	–	3.2	–
7801-87.32.7	6.2	3.4	1.7	0.66	0.33	1.8	–	3.2	–
7803-80.60	5.9	3.4	1.8	0.72	0.40	2.0	–	3.1	–
7511-83.55	6.9	4.2	2.4	0.92	0.56	2.8	–	4.1	–
SCBS-4-103	7.5	4.3	2.7	0.96	0.58	2.9	3.0	4.3	–
7606-Los Angeles Bight, CA	8.9	4.7	2.9	1.2	0.80	3.7	3.7	5.0	–
6204-133.25	9.2	4.8	3.1	1.2	0.76	3.7	3.7	4.8	–
6707-117.30	10.2	5.5	3.6	1.4	0.84	4.6	4.2	5.5	4.0
5707-137.35	12.0	5.6	4.4	1.4	1.2	5.4	5.0	6.0	damaged
TC50-sta. 28	13.0	6.0	4.8	1.7	1.3	6.5	5.2	7.0	4.6
7803-73.50	15.2	7.3	5.5	2.2	1.1	6.8	5.4	7.6	6.2
7510-117.30	18.0	7.4	5.8	2.4	1.2	8.5	6.8	8.3	7.2
7510-117.30	19.6	9.4	6.0	2.3	1.4	9.4	7.4	9.1	6.9
7808-MWT22	21.3	9.9	6.7	3.0	1.9	10.3	7.4	10.4	8.0
6402-140.30	23.0	10.5	7.5	3.0	1.9	11.7	9.2	10.5	9.2
LACM 9659-7 Mex. Cedros Isl.	27.9[2]	12.9	9.6	3.2	1.5	14.0	9.8	13.4	11.0
SIO H52-221	28.6	14.1	10.0	3.2	2.2	13.4	11.2	13.7	12.1
SWFC reared	33.6[2]	14.3	12.2	4.8	2.2	17.8	13.3	16.8	12.4
LACM 9659-7, Mex. Cedros Isl.	36.0[2]	17.0	12.0	4.9	2.1	17.0	12.0	17.4	14.5
C6208-Cobb 55-18	45.9[2]	19.9	13.9	4.4	3.1	22.5	16.2	20.5	15.0
SIO 60 409.42A	47.0[2]	19.0	15.8	5.3	3.6	20.6	15.9	18.2	17.3

[1] Specimens between dashed lines are undergoing notochord flexion.

[2] Juvenile.

TABLE 2

Body Proportions of Larval and Juvenile *Peprilus simillimus*.[1]

Body proportion	N	Snout to anus / body length	Head length / body length	Eye diameter / head length	Snout length / head length	Body depth at pectoral fin base / body length	Snout to dorsal fin / body length	Snout to anal fin / body length	Snout to pelvic spine / body length
Preflexion ...	7	54.4±3.9 (49-60)	22.0±4.8 (14-27)	46.8±9.4 (38-64)	23.4±4.5 (18-30)	25.2±4.5 (22-33)	–	–	–
Flexion	6	55.4±1.06 (54-57)	28.8±1.5 (28-31)	37.6±1.0 (36-39)	21.4±1.6 (19-23)	29.8±2.3 (27-34)	–	53.5±0.6 (53-54)	–
Postflexion ...	10	51.5±5.6 (41-61)	35.0±1.8 (32-38)	37.2±2.9 (32-41)	23.5±2.2 (21-27)	43.5±3.6 (38-50)	39.9±1.8 (36-42)	53.0±4.0 (46-59)	38.9±2.1 (35-41)
Transforming	4	47.4±1.63 (46-49)	32.4±1.9 (31-35)	38.6±5.0 (32-44)	25.0±2.7 (22-29)	48.5±1.7 (47-51)	38.0±2.3 (35-40)	47.2±1.4 (46-49)	38.8±3.1 (32-42)
Juvenile	5	43.9±2.76 (40-47)	33.6±2.2 (30-36)	35.7±4.1 (32-41)	19.2±3.2 (16-23)	48.6±3.4 (44-53)	35.4±2.5 (33-40)	46.0±4.5 (39-50)	37.2±2.9 (33-39)

[1] Values are expressed as percent of body or head length (mean, standard deviation, and range).

TABLE 3
Meristics of Cleared and Stained Larvae of *Peprilus simillimus*.[1]

Size (mm)	Dorsal fin	Anal fin	Pectoral fin	Pelvic spine	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers
4.2	–	–	–	–	–	–	2	–
4.8	–	–	–	–	–	–	–	–
5.8	–	–	–	–	3+2	–	5	–
6.2	16	16	10	–	0+9+8+1	–	6	–
6.5	19	16	9	–	0+8+8+1	–	6	4
7.1	36	37	13	–	3+9+8+3	–	6	6
7.8	I, 35	0, 32	13	–	2+9+8+2	–	6	8
9.7	II, 46	II, 42	17	damaged	5+9+8+4	13+17=30	6	10
10.5	III, 43	II, 38	19	spine bud	5+9+8+5	13+17=30	6	5
12.0	III, 44	II, 39	18	✓	6+9+8+6	13+17=30	6	0+14
12.4	II, 45	II, 40	19	✓	5+9+8+4	13+17=30	6	0+11
13.9	III, 45	II, 42	21	✓	7+9+8+6	13+17=30	6	0+11
15.0	III, 46	II, 42	19	✓	6+9+8+6	13+17=30	6	0+12
17.0	III, 46	II, 42	19	✓	7+9+8+6	13+17=30	6	1+13
18.8	III, 44	II, 40	20	✓	7½+9+8+7	13+17=30	6	3+13
20.0	III, 46	III, 40	21	✓	6+9+8+6	13+17=30	6	3+11

[1]Specimens between dashed lines are undergoing notochord flexion. Check indicates presence of pelvic spine.

They begin to form at about 6.5-mm length and become incorporated into the preopercular bone by about 14-mm length. The number of observed spines ranged from one in the small sizes to as many as nine seen in a 12-mm specimen.

Fin Formation and Internal Structures

The caudal, pectoral, dorsal, and anal fin rays begin to ossify towards the end of the notochord flexion phase (Table 3). The adult complement of 9+8 principal caudal rays is ossifying before notochord flexion is complete. The full ray complements are ossifying in the pectoral (19-23), dorsal (II-IV, 41-48), and anal (II-III, 35-44) fins at about 10.0-mm length. Pelvic fins are represented by a single minute spine projecting from near the distal end of the pelvic bone. The pelvic bone begins to ossify at about 9.5-mm length and the pelvic spine at about 10 mm. Ossification of the vertebral column begins after the completion of notochord flexion, and the full complement of 29-31 vertebrae is ossifying by about 10.0-mm length. The stellate teeth of the pharyngeal sacs begin ossifying at about 7.1-mm length, and most are present by about 9.7-mm. The three predorsal bones begin to ossify at about 9.7-mm length. These interdigitate with the neural spines such that they precede the first, second, and third neural spines. Scales on the lateral line begin forming at about 19-mm length, marking the beginning of transformation. The smallest completely scaled specimen seen was 27.9 mm.

Pigmentation

Yolk-sac larvae have melanophores on the snout, around the eyes, on the anterior region of the yolk-sac, on the anterior surface of the oil globule, just above the gut on each side, along the ventral midline from the anus to the notochord tip, and at the margin of the dorsal finfold above the trunk (Figure 1). A characteristic median dorsal pigment structure, on about the 16th myomere, can be seen in the earliest stages and persists through larval development. This structure is composed of 1-6 pigment clumps and in yolk-sac larvae is usually slightly above the dorsum in the finfold. It is associated with an opaque zone in the surrounding finfold and may be a large melanophore or a complex of small ones.

After yolk absorption, melanophores fill in around the dorsal spot and down the side of the trunk and gut towards the head so that the anterior half of the trunk is fairly well pigmented by about 3.0-mm length. The head, nape, and dorsum are bare of pigment (Figure 1). A median ventral line of pigment extends from the cleithrum to the anus at this stage. The head is usually pigmented on the isthmus, at the symphysis of the lower jaw, over the brain, and internally on the floor of the cranium.

As development continues, the lateral melanophore zone extends posteriorly and the unpigmented nape and dorsum gradually become covered (Figures 2 and 3). The dorsal aspect of the head becomes solidly pigmented, whereas the cheek region remains relatively unpigmented (Figure 3). By 12-mm length, 70% of the body is covered by melanophores, and some pigment can be seen over the hypural plates. The pectoral fin has a few melanophores at the fin base and some which extend out onto the upper rays. At 15-mm length, 90% of the body is pigmented, leaving only the caudal peduncle unpigmented. By 20-mm length, the caudal peduncle is completely pigmented, and melanophores are present over the hypural region as well as at the base of the caudal fin rays. Pigment forms in the anterior part of the dorsal and anal fins in a narrow band adjacent to the base of the rays. It gradually spreads posteriorward and also increases in width. In juveniles the pigmented area on the dorsal fin extends over much of the fin. The pigmented zone on the anal fin is narrowest and extends out on the fin for a third or less of its width. Pigment gradually spreads throughout the caudal fin, but the individual melanophores are smaller and their distribution is less dense than on the dorsal and anal fins.

DISTRIBUTION

Larvae of *P. simillimus* occur in comparatively low numbers in CalCOFI samples (Ahlstrom 1965); however, this may reflect the relatively low sampling effort in the nearshore region inhabited by this species. Horn (1970) summarized the geographic and seasonal distribution of *P. simillimus* larvae sampled by CalCOFI during 1955-59 and showed that larvae are taken at coastal stations from Point Conception, California, southward to the vicinity of Bahia Magdalena, Baja California. Larvae occurred in the samples throughout the year but were collected in greatest number during May, June, and July. Greatest larval catch was in upper central Baja California in the vicinity of Bahia Sebastian Viscaino (ca. 28°N).

The distribution and relative abundance of *P. simillimus* larvae on CalCOFI cruises during 1975 (Figure 4) was similar to 1955-59. Larvae occurred from Point Conception south to Bahia Magdalena with three major areas of concentration; i.e. the Southern California Bight, Bahia Sebastian Viscaino area, and in the bight north of Bahia Magdalena. These are regions where the shelf is relatively broad with a mud or sand substrata. The enlarged adult habitat in these regions (contrasted with intervening regions that have narrow shelves) is reflected by greater larval catch and more extensive offshore larval distribution (Figure 4). Relative abundance and extent of offshore distribution are greatest in the Bahia Viscaino area were the shelf is broadest.

In 1975 the number of *P. simillimus* larvae reached a peak during summer cruises, but larvae occurred relatively frequently on the October cruise. In fact, cruise 7510 (October 1975) accoumted for 45% of the total occurrences for the year. During 1955-59 almost no *P. simillimus* larvae were taken after August, and occurrences during the October cruises of 1955-59 accounted for 2% of the total occurrences.

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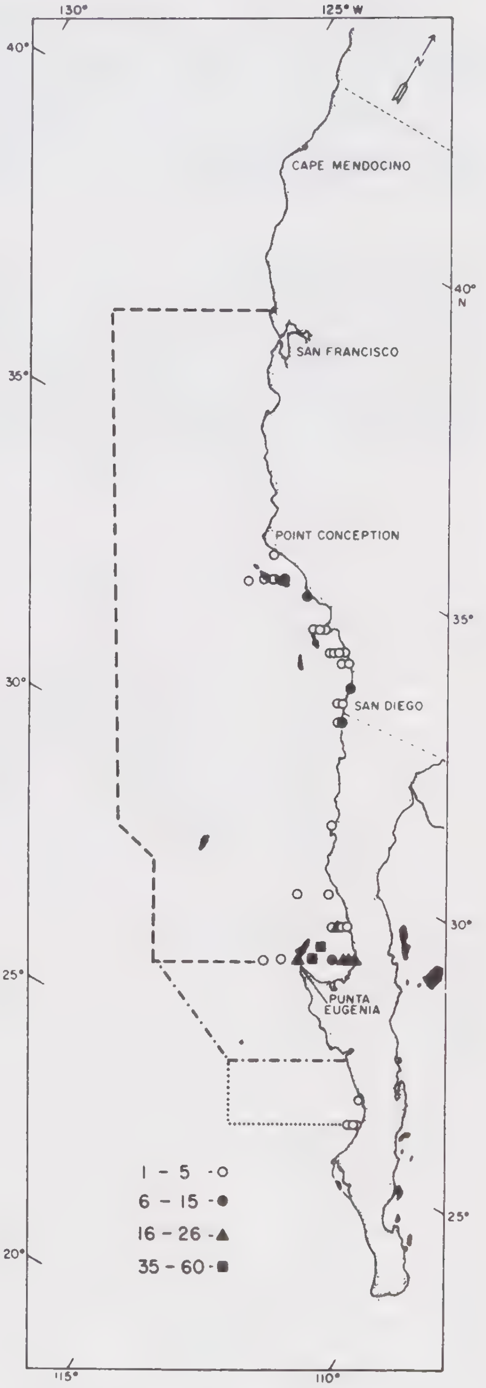

Figure 4. Distribution of total catch of *Peprilus simillimus* larvae collected on five CaLCOFI cruises during 1975. Legend indicates actual numbers of larvae taken on each CalCOFI station. Dashed lines indicate approximate area sampled by five cruises. More southerly areas were sampled by four (. __ .) and by three (. . .) cruises.

produced the original wash drawings of four of the larvae from which tracings were made. Henry Orr provided drafting assistance. We are grateful to Morgan Busby, John Butler, Richard Charter, Elaine Sandknop, Betsy Stevens, and Barbara Sumida-MacCall for advice and assistance during the preparation of the manuscript. Kate Coleman and Lorraine Prescott typed drafts of the manuscript.

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8019

Accumulation of ^{14}C Labeled Benzene and Related Compounds in the Rotifer *Brachionus plicatilis* from Seawater

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ECHEVERRIA, T. 1980. Accumulation of ^{14}C labeled benzene and related compounds in the rotifer *Brachionus plicatilis* from seawater. Can. J. Fish. Aquat. Sci. 37: 738–741.

Rotifers were exposed to (1) a single dose of ^{14}C labeled benzene on day 1 with initial concentrations of benzene at 0.1 and 1.0 μL/L declining over time and (2) a chronic exposure of 0.1 and 1.0 μL/L daily for 9 d. Both conditions resulted in rotifers accumulating 1000 to 10 000 times the ^{14}C activity detected in the seawater. These concentrations were maintained in the rotifers for 8 and 11 d, respectively, and remained high even after exposure was terminated. Analysis of ^{14}C activity from ^{14}C labeled benzene detected in the water revealed its source to be phenolic compounds, compounds with a potentially higher toxicity than benzene. The water maintained a low level of ^{14}C compounds throughout the experiments. Rotifers accumulated high quantities and retained most of the acquired ^{14}C compounds after 2 d in clean water.

Key words: benzene, rotifer, zooplankton, biomagnification

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Des rotifères furent soumis à (1) une exposition à une seule dose de benzène marqué au ^{14}C au jour 1, de concentrations initiales de benzène de 0,1 et 1,0 μL/L, diminuant avec le temps, et (2) une exposition chronique à 0,1 et 1,0 μL/L quotidiennement pendant 9 jours. Dans les deux situations, il en est résulté chez les rotifères une accumulation de 1 000 à 10 000 fois l'activité du ^{14}C décelée dans l'eau de mer. Ces concentrations se maintiennent chez les rotifères pendant 8 et 11 jours, respectivement, et demeurent à un niveau élevé même une fois l'exposition terminée. L'analyse de l'activité du ^{14}C dans le benzène marqué au ^{14}C décelée dans l'eau montre qu'elle a comme source des composés phénoliques, composés d'une toxicité potentiellement supérieure à celle du benzène. Durant toutes les expériences, l'eau conserve un bas niveau de composés de ^{14}C. Les rotifères accumulent de fortes quantités et conservent la plus grande partie des composée de ^{14}C acquis, après 2 jours en eau propre.

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METABOLISM of petroleum hydrocarbons by animals requires certain NADPH-dependent enzymes (Sims and Grover 1974). Many marine fish and invertebrates are able to metabolize hydrocarbons (Varanasi and Malins 1977). Some marine phytoplankton and invertebrates are unable to metabolize specific hydrocarbons because they do not possess the necessary enzymes. The ability of clams (Neff and Anderson 1975), mussels (Clark and Finley 1975; Lee et al. 1972), barnacles (Morris 1973), oysters (Stegeman and Teal 1973), and jellyfish (Lee 1975) to accumulate oil components, but not to metabolize them, stimulated my interest in biomagnification through the food chain.

The cosmopolitan euryhaline rotifer *Brachionus plicatilis* is easily reared in the laboratory and has proven to be adequate as larval fish food (Theilacker and McMaster 1971). It is now used in the Tiburon Laboratory to rear larval fishes (Struhsaker et al. 1974).

Benzene, a monocyclic aromatic hydrocarbon of the water-soluble fraction of crude oil, has a low toxicity (Hawley 1971) and is soluble in seawater at 1400 μL/L (Benville and Korn 1977). Benzene occurs chronically in the open ocean and in estuaries at about 0.001 to 0.1 μL/L (Lee and Ryan 1976).

To determine the fate of a single component of crude oil in a prey species, I studied the uptake and depuration of benzene in *B. plicatilis* exposed to experimental concentrations of benzene that approximated measured environmental levels.

Methods — A culture of *B. plicatilis* was maintained in an 80-L glass aquarium under constant aeration, illumination (Grolux[1] and fluorescent lights at 215 lx), salinity (20‰ ± 2‰), and temperature (22 ± 2°C). They were fed a 2-μm-long green flagellate (*Nephroselmis* sp.: 10^4 cells/mL) reared under identical conditions, except for a higher light intensity (1615 lx). The rotifers were fed daily for 1 wk before experiments to ensure a healthy population, but not during the experiment.

Double cellulose-filtered (pore size 5 μm) and 8-L single charcoal-filtered seawater was placed in green, 10-L poly-

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service (NOAA).

ethylene pans. The static pans were kept in a water bath at constant light (24 h: 108 lx), temperature (14–16°C), and salinity (23‰). Rotifers were concentrated on a 53-μm Nitex nylon net, rinsed with clean, filtered seawater, and transferred to the experiment pans. Rotifer populations were monitored daily using a model ZBI Coulter counter. Rotifer dry weights were obtained by rinsing with distilled water, drying at 20°C for 24 h, and weighing on a Cahn model 4400 electro-balance ($\pm$0.1 μg). The average weight for a rotifer was 0.35 μg. [^{14}C]benzene solution was prepared by combining a benzene stock solution with ^{14}C labeled benzene. The saturated benzene stock solution was prepared by vigorously shaking 99.9% benzene into 1 L of filtered seawater. The concentration was measured on a Tracor MT220 gas chromatograph (GC) (Benville and Korn 1974). An appropriate amount of stock solution was combined with ^{14}C labeled benzene to give the desired specific activity, and then stirred into pans for final concentrations of 0.1 or 1.0 μL/L. [^{14}C]benzene solution activities were monitored by sampling 1 mL from the center of each pan, mixing it with 10 mL Instagel® scintillator, and counting it on a Packard liquid scintillation spectrometer. The activity of experimental seawater was similarly measured daily, before and after the addition of fresh [^{14}C]benzene solution. Initial measurements were used to calculate how much, if any, new [^{14}C]benzene solution is needed to maintain specific activities of 10 and 100 in expt. 1, and 12 and 122 in expt. 2. Water samples were measured on a gas chromatograph (GC) on days 1, 3, and 5 to determine actual amounts of benzene (Fig. 1).

The activity in rotifers was counted by concentrating up to 500 mL of rotifers, or ~0.02 mg on a 53-μm net, washed into a beaker with 10 mL of water, and transferred to a Pasteur capillary pipet plugged at the base with glass wool. Packard-100® solution digestor was added (0.5 mL), and the pipet sealed for 25 h at 20°C. The digest was transferred to a scintillation vial with 10-mL Dimulene® scintillator by using air pressure and then flushing the pipet twice with the scintillator. Samples were counted and corrected for a total method efficiency of 61%, determined by running a known concentration of [^{14}C]benzene through the sampling method.

In expt. 1, rotifers (60/mL) were given a single initial dose on day 1 and left in the dosed pans for 8 d. The contents of two replicate pans for each concentration of benzene, 0.1 and 1.0 μL/L, were monitored daily for ^{14}C activity in the water column and in the rotifers.

In expt. 2, rotifers (20/mL) were exposed to benzene concentrations at relatively constant levels of 0.1 or 1.0 μL/L for 9 d. Because about 70% of the [^{14}C]benzene volatilizes in 24 h (Eldridge and Echeverria 1977), concentrations remaining 24 h after dosing were brought up to the target level by adding [^{14}C]benzene solution equivalent to the amount volatilized. ^{14}C activity in the water was measured daily with the scintillation counter. During the second experiment, the actual concentration of benzene was determined every 2 d with a gas chromatograph for the two replicates of each concentration.

Results — In experiment 1, 80% of ^{14}C was lost from the water to the air, pan surfaces, and rotifers at both initial concentrations of [^{14}C]benzene after 2 d. However, ^{14}C compounds never completely disappeared from the aqueous phase (Fig. 1).

In experiment 2, [^{14}C]benzene was administered to maintain an actual level of ^{14}C activity in the seawater of 0.12 ($\pm$0.04 μL/L) and 1.1 ($\pm$0.5 μL/L) (Fig. 1) for 9 d. Actual concentration of benzene monitored by the gas chromatograph (GC) was compared to ^{14}C activity monitored by the scintillation counter. On day 1, measurements by both techniques corresponded to the target concentrations of benzene; however, by day 5, the GC failed to detect any benzene in the system while the scintillation counter was showing ^{14}C activity. [^{14}C]benzene solution was added to the experimental pans to maintain the concentration of [^{14}C]-benzene monitored by the scintillation counter. For the duration of these experiments the presence of benzene and of ^{14}C activity were not correlated. Water samples from a pan with a benzene concentration of <0.01 μL/L (GC) and a ^{14}C count corresponding to 0.8 μL/L were sent to an analytical laboratory. Method C (Taras et al. 1971), a standard method for the determination of phenols, indicated that all ^{14}C activity (0.8 μL/L) was due to phenolic compounds. This method includes possible interference from benzene; however, no benzene was detected by GC with a sensitivity of 0.01 μL/L.

Adsorption was measured by taking water samples from the cleaned and refilled pans on day 9, and showed ^{14}C activity of 0.001 μL/L. The only source of ^{14}C would be leaching from the container walls into solution.

In expt. 1, the rotifers accumulated ^{14}C compounds rapidly (Fig. 1), reached an asymptote by day 5, and were maintained for the duration of the experiment. Final biomagnification of ^{14}C compounds in the rotifers on day 8 were 10^2 times, at 0.1 μL/L, and 10^3 times at 1.0 μL/L, the levels in the water. The rotifers accumulated and maintained a high level of ^{14}C compounds which did not appear to be depurated while in the treated water.

In expt. 2, the rotifers under chronic exposure accumulated a maximum of ~10^4 times the initial concentration in the water. A peak in the rotifers was reached on day 6 during which time the benzene (GC) was not present in the water.

Both singly (initial dose) and chronically (constant dose) treated rotifers accumulated ^{14}C compounds to high concentrations. The data suggest that there is a limit to the amount of ^{14}C compounds a rotifer is able to store, with a state of equilibrium being reached between the water and the rotifers. ^{14}C compounds never completely left either system during the 8- or 11-d experimental periods.

Discussion — The presence of phenols in the experiments, instead of benzene, indicates some type of chemical degradation. The stability of benzene and the short duration of these experiments would eliminate photochemical oxidation occurring at any significant level. Possibly the benzene was metabolized by bacteria. Biodegradation of benzene has been demonstrated with in situ marine microbes (Lee and Ryan 1976), specifi-

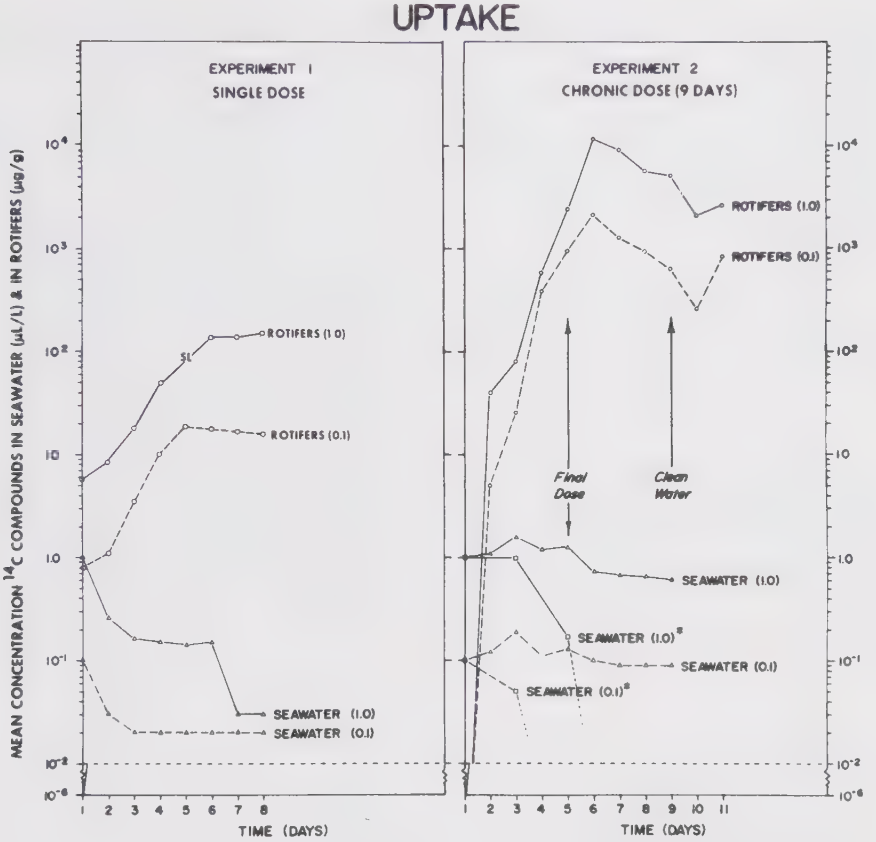

FIG. 1. Expt. 1. Uptake of ^{14}C compounds by the rotifer *B. plicatilis* and the corresponding concentration in the seawater. Expt. 2. Uptake of ^{14}C compounds by *B. plicatilis* under chronic exposure, and the corresponding concentration in the seawater. Values in the seawater measured daily on a scintillation counter and on days 1, 3, and 5 on a gas chromatograph (GC). *GC analysis, concentration of benzene approaches 0 between measurements; solid lines are 1.0 µL/L; broken lines are 0.1 µL/L.

cally the bacteria *Pseudomonas putida* (>1.0 µm long) and *Nocardia* sp. (>1.0 µm long) (Gibson 1976). It is not known whether any marine microbes capable of benzene degradation were present in the experimental pans. To determine if ^{14}C activity was bound to bacteria, a subsample of water from all pans was filtered through 0.45-µm Millipore filter paper and analyzed on the scintillation counter. ^{14}C activity for unfiltered water corresponded to that of the filtered water samples measured on the same day. Therefore, ^{14}C was not bound up in any particle or bacteria larger than 0.45 µm. If the benzene was degraded by bacteria, it was not bound to them.

Biodegradation of benzene by the experimental animals is also a possibility; however, hydrocarbons stored for long periods indicate the inability of animals to metabolize them (Lee 1975). During these experiments, rotifers accumulated and maintained concentrations of benzene and phenolic compounds many times the exposure level. It is possible that the rotifers were metabolizing benzene into phenols, but because ^{14}C compounds were retained by them, the effect is still the same: rotifers accumulated and retained concentrated amounts of ^{14}C compounds during the experimental time frame. Depuration may occur in clean water over a longer time than tested.

Herring larvae exposed to ^{14}C compounds through water accumulated 2 times the concentration in the water, increasing to 3.2 times when fed the rotifer (Eldridge et al. 1978). The ability of the rotifer to accumulate benzene results in the availability of a higher concentration of benzene and related compounds to feeding larval fish, and would increase the possibility of adverse effects. Larval herring showed alterations in their metabolic process when exposed to benzene at 0.02–2.3 µL/L (Eldridge et al. 1977). Juvenile herring assimilate labeled hydrocarbons in the stomach tissue and lipids (Whittle et al. 1977), with unknown consequences. Depuration of hydrocarbons in fish does occur, and depuration of ^{14}C compound in rotifers is an untested possibility. However, rotifers accumulate high concentrations of ^{14}C compounds, larval herring accumulate ^{14}C compounds when feeding on rotifers, and there are metabolic changes in larvae. Just because the fish can metabolize ^{14}C compounds does not eliminate possible adverse effects when both the fish and its food are exposed to the hydrocarbon.

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AN INVESTIGATION INTO UNUSUAL MORTALITY IN THE HAWAIIAN MONK SEAL, *MONACHUS SCHAUINSLANDI*

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ABSTRACT

Increased mortality was reported in the endangered Hawaiian monk seal population at Laysan Island in the spring of 1978. An investigation of the possible causes of the mortality included sampling of healthy, sick, and dead individuals. Analyses comprised gross and microscopic pathology, hematology, serum chemistry, virology, bacteriology, parasitology, and toxicology. Gastric ulceration in varying degrees due to nematodes was a consistent finding. Evidence of caliciviruses (VESV and SMSV) and *Salmonella* was found in the population. Two of 18 seals tested had elevated total white blood cell counts. A few individuals differed significantly from mean serum chemistry values but no trend was apparent. Liver tissues of two seals tested for ciguatoxin and maitotoxin were positive.

Monachus schauinslandi
mortality
clinical pathology
ciguatera

INTRODUCTION

The Hawaiian monk seal, *Monachus schauinslandi*, is an endangered species which breeds only in the Northwestern Hawaiian Islands from

Necker Island west to Kure Atoll. Recent censuses indicate the total population has decreased by about 50% since 1958 (Johnson et al., in preparation).

In the spring of 1978, high mortality was observed in monk seals at Laysan Island (B.W. Johnson and P.A. Johnson, Aquatic Mammals Behavioral Research Company, Honolulu, Hawaii 96822, personal communication, 1978). Disease signs apparent in the monk seals were consistent. Animals come ashore emaciated or began to noticeably lose weight as they lay on the beach. The seals abandoned normal hauling out behavior--failing to move into the vegetation behind the beach crest at night. Within 2 to 3 weeks of beginning the weight loss, the animals became completely debilitated and then died in the splash zone or at the high tide line (B.W. Johnson and P.A. Johnson, personal communication, 1978).

This report discusses data collected on specimens taken from 19 dead and 18 live monk seals during April and May 1978 as part of an investigation into the reported mortality.

MATERIALS AND METHODS

Between 4 May and 13 May 1978 we collected specimens and data from a total of 24 Hawaiian monk seals at two locations in the Northwestern Hawaiian Islands to determine if there was any apparent disease process in the seals which might cause the mortality. Ten live yearlings or juvenile seals (MS-01-78 to MS-10-78) and one adult (MS-11-78) were sampled at Laysan Island. In addition, we received tissue sets in formalin[1] from 13 monk seals (collected by Brian W. and Patricia A. Johnson on Laysan Island, 1 March to 1 May 1978) which died at Laysan Island prior to our arrival. Samples were to be collected from a large number of sick as well as apparently healthy animals; however, a storm just prior to our arrival cleared the beaches at Laysan Island of most of the very sick animals with the disease signs mentioned earlier. Seal MS-11-78 was very emaciated and weak and died while being restrained for collection of the samples. At French Frigate Shoals six dead seals were found, only one of which was fresh enough to be necropsied, even through it had been dead at least a day and the tissues were badly autolysed. The other five were too decomposed to yield any information relative to cause of death.

The live animals were physically restrained and blood was collected from the intra-vertebral extradural vein. Packed red cell volumes and white blood cell counts were determined in the field. Serum and plasma for the other clinical bood tests and serological studies were frozen for later analysis. Clinical chemistry tests were performed using standard laboratory procedures (Bio-Science Laboratory, Van Nuys, California). Serum samples from all animals were tested for agglutinating antibodies to Leptospira antigen pools nos. 1, 2, and 3.[2] They were also tested for serum neutralizing (SN) antibodies to 19 calicivirus types (vesicular exanthema of swine virus types A_{48}, C_{52}, D_{53}, F_{54}, G_{55}, I_{55}, J_{56}, K_{56}, San Miguel sea lion virus types 1, 2, 4, 5, and marine calicivirus isolates designated 427, 274, fluke, V86, 804T, and 913T) using previously described microtiter techniques (Monta and Bryon, 1974; Smith et al., 1976).

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Leptospira isolation attempts were made on samples of liver, kidney, and cerebrospinal fluid taken from MS-11-78. The procedure has been previously described (Smith et al., 1974a; Smith et al., 1974b).

Salmonella incidence in the seals was tested by collection of rectal swabs from all animals and placing them into transport medium in the field. These cultures were tested by one of the authors (Gilmartin) for salmonellae by beginning enrichment and isolation procedures previously described (Gilmartin et al., 1979) within 24 hours of collection of the sample but were also maintained in the holding medium for over 2 weeks, when another attempt was made at isolation of salmonellae (N.A. Vedros, Naval Biosciences Laboratory, Oakland, California 94625, personal communication, 1978).

Swabbings were taken from the nose, throat, and rectum of each animal for virus isolation. These and small slips of lung, liver, kidney, and tonsil from animal no. 11 were placed in ampules of phosphate-buffered glycerine, pH 7.2, and immediately frozen to -55°C. Tissues were thawed and ground up, then they and the swab samples were clarified by centrifugation at 3,000 rpm. Supernatant fluids were placed in a Vero monkey, Cercopithicus aethiops, kidney cells and porcine kidney cells (PK-15), incubated at 37° and 30°C, and passaged at least four times as previously described (Smith et al., 1974b).

Stool specimens were collected, as available, from the seals and frozen for later flotation and examination for ova.

Rectal temperatures were determined using an electronic thermistor with a flexible probe inserted at least 30 cm through the rectum.

Tissues for microscopic histopathologic studies were preserved in formalin and examined after hematoxylin and eosin staining.

One canine tooth was extracted from each of the dead seals for aging using a new technique developed for small cetaceans (Pierce and Kajimura, 1978).

Liver specimens from two seals (MS-11-78 and MS-12-78) were assayed for dioxan (2, 3, 7, 8 - tetrachlorodibenzo-p-dioxan) using gas chromatography and high resolution mass spectrometer techniques (M. Gross, University of Nebraska, Lincoln, Nebraska 68588, personal communication, 1978.)

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[2] Difco Laboratories, Detroit, Michigan. These pools contain Leptospira ballum, L. canicola, L. icterohemorrhagiae, L. bataviae, L. grippotyphosa, L. pyogenes, L. autumnalis, L. pomona, and L. wolffii.

Tests for tissue residues of ciguatoxin by radioimmunoassay procedures (Hokama et al., 1977) and ciguatoxin and maitotoxin by bioassay techniques were performed.[3]

Statistical analyses were performed on the clinical chemistry, hematology, and temperature data to test for individuals with values different than the mean. All the live seals sampled with one exception were young (yearlings to juveniles); therefore the adult (MS-11-78) was excluded from these statistical tests and the mean and standard deviation of the data from these animals were taken as a close approximation to parametric values since normals for the population were not known. The farthest-outlying variates within a given sample (i.e., sodium) were then tested to see if they statistically belonged within that sample using a one-tailed t-test of one variate against the assumed population mean (Sokal and Rohlf, 1969). Also, because of the great distance between the islands (approximately 320 nmi), the data for the young monk seals from Laysan Island (MS-01-78 through MS-10-78) were tested with a two-tailed Wilcoxon two-sample test (Sokal and Rohlf, 1969) against those from French Frigate Shoals (MS-13-78 through MS-19-78) for all categories to determine if there were differences between the island populations.

RESULTS AND DISCUSSION

Animals from two age groupings, the young and very old, were represented in the dead animals which were recovered by the Johnsons and the authors. Ten of 14 seals which died and were recovered at Laysan Island were between 1 and 5 years of age; the others were between 18 and 30 years. The net loss in monk seals at Laysan Island during the period from March to July 1978 is estimated to be at least 50 animals (Johnson and Johnson, 1980).

Of the 13 seals which had died prior to our arrival at Laysan Island and from which we received tissue sets, there were seven males and six females. Four of the six dead seals at French Frigate Shoals were females and sex could not be determined for the other two.

Twelve of the live young monk seals sampled were females, five were males and the single adult at Laysan Island (MS-11-78) was a male. Four of the seals sampled at Laysan Island (MS-01, MS-04, MS-07, and MS-10) became emaciated and disappeared by mid-June 1978. The seals sampled at French Frigate Shoals were not similarly monitored.

Statistical tests were performed on the clinical data to identify animals with test results significantly different ($P \leq 0.05$) from the mean of all monk seals sampled. The tests were done to aid in recognizing ill animals in a species for which these clinical parameters had not been determined.

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[3] Radioimmunoassay for ciguatoxin and bioassay for ciguatoxin and maitotoxin were performed by Dr. Y. Hokama and Dr. J. Miyahara, respectively, at the University of Hawaii, John A. Burns School of Medicine, Pathology Department, Honolulu, Hawaii 96822.

When each individual seal's hematology and clinical chemistry test results were compared to the mean of the group, many had at least one test value different from the mean (Table 1). There were only three cases where two animals differed from the mean ($P \leq 0.05$) in the same direction on the same test: MS-05 and MS-07, elevated total white cell count; MS-06 and MS-18, high cholesterol; and MS-08 and MS-15, high alpha-1 globulin.

Monk seals MS-05 and MS-07, with the high white cell counts, are noteworthy because MS-07 is one of four animals which disappeared and presumably died later in the season. MS-07 had the highest white cell count (18,700) of all seals tested and was one of three young seals sampled which appeared underweight and lethargic. Neither of these two with the elevated total white cell counts had any other outstanding clinical data values. Of the other two monk seals which appeared underweight at sampling, one (MS-06) had only a significantly elevated cholesterol and glucose level, which may indicate a fasting animal, and the other (MS-01) had no clinical blood tests different from the mean of the group.

The three other animals which disappeared in an emaciated condition during the summer, MS-01, MS-04, and MS-10, did not exhibit any remarkable findings except for a high lactic dehydrogenase (LDH) in MS-10.

The only other animals with any noteworthy abnormal clinical pathology were MS-09 with a high total protein and beta globulin and MS-16 with a very low packed red cell volume and a high serum glutamic pyruvic transaminase (SGPT). Salmonella sieburg was isolated from a rectal swab taken from MS-09 and it is the only seal from which salmonellae were recovered (N.A. Vedros, personal communication, 1978). Although Salmonella are common isolates in some pinnipeds (Gilmartin et al., 1979), the high beta globulin and total protein in this animal are probably not related to a chronic infectious bout with this organism as no serum antibody could be detected (N.A. Vedros, personal communication, 1978).

The high SGPT of MS-16 would indicate some liver pathology. The low hematocrit may be due to hemorrhage associated with severe gastric ulceration due to nematode infestation which will be discussed below. Despite the frequency and apparent severity of these parasitic ulcerations observed in dead animals, MS-16 was the only living seal tested which had a low packed cell volume.

The rectal temperature statistics in Table 1 show that all animals tested were within a range of 1.5°C. All of these animals were asleep and dry when initially approached so there had probably been little or no physical activity prior to our restraining them. Thus, these temperatures (with a mean of 36.3°C) reflect resting status, and are very close to that previously reported for young Hawaiian monk seals. Several monk seals were monitored throughout the restraint period, and no change in the temperature reading was noted. Temperatures taken by various means in some other phocids are reported between 36.0°C and 37.0°C.

TABLE 1. SERUM CHEMISTRY, BLOOD COUNTS, AND RECTAL TEMPERATURE STATISTICS FROM 17 YOUNG HAWAIIAN MONK SEALS, 1978

Test	Mean	Standard Deviation	Range	Animals Significantly Different at $P \leq 0.05$	
Sodium (meq/liter)	152.7	8.1	134-167	MS-08 (134)	MS-18 (167)
Potassium (meq/liter)	5.84	0.63	4.6-7.0	MS-03 (7.0)	MS-08 (4.6)
Chloride (meq/liter)	108.7	4.8	96-119	MS-08 (96)	MS-13 (119)
Calcium, total (meq/liter)	5.54	0.37	5.0-6.1		
Inorganic phosphorus (mg/100 ml)	7.49	1.49	5.3-9.6		
Cholesterol (mg/100 ml)	206.7	54.5	121-314	MS-06 (314)	MS-18 (311)
Urea nitrogen (mg/100 ml)	37.1	12.3	21-63	MS-17 (63)	
Uric acid (mg/100 ml)	2.74	0.51	1.7-3.4	MS-02 (1.7)	
Bilirubin, total (mg/100 ml)	0.38	0.28	0.2-1.2		
Alkaline phosphatase (units)	222.0	131.2	74-580		
LDH (units)	758.9	454.7	62-1,640		
SGPT (units)	137.8	57.6	76-290	MS-16 (290)	
SGOT (units)	146.9	45.7	72-220		
Glucose (mg/100 ml)	91.1	24.6	49-141	MS-06 (141)	
Total protein (g/100 ml)	7.32	1.01	4.9-9.5	MS-09 (9.5)	
Albumin (g/100 ml)	2.82	0.36	34		
Alpha-1 globulin (g/100 ml)	0.32	0.33	0.08-1.2	MS-08 (1.2)	MS-15 (0.9)
Alpha-2 globulin (g/100 ml)	1.09	0.53	0.4-1.96		
Beta globulin (g/100 ml)	0.80	0.25	0.4-1.3	MS-09 (1.3)	
Gamma globulin (g/100 ml)	2.30	0.57	1.3-3.4	MS-06 (3.4)	MS-08 (1.3)
Albumin/globulin ratio	0.64	0.09	0.5-0.8		
Packed red cell volume (5)	57.1	4.0	46.0-62.5	MS-16 (46.0)	
White cell count, total (cells/mm^3)	9,745	3,178	5,170-18.700	MS-05 (15,400)	MS-07 (18,700)
Rectal temperature (°C)	36.3	0.54	35.5-37.0		

Rectal swab cultures from more than half of the animals yielded *Edwardsiella tarda* which is of dubious significance as an intestinal tract pathogen.

Neither viruses nor leptospires were isolated from any sample; however, animal MS-05 did carry SN antibodies against VESV I_{55} at the 1:40 dilution and animals MS-13 and MS-19 carried SN titers of 1:10 against SMSV-1. All other tests for virus and *Leptospira* antibodies were negative; however, the finding of calicivirus antibodies (VESV and SMSV) in 3 of 18 animals certainly suggests occasional contact with these agents and may be some indication that virus reservoirs exist along the Northwestern Hawaiian Islands chain. Alternatively, northern elephant seals, *Mirounga augustirostris*, have been reported as far west as Midway Islands (M.J. Rauzon, National Fish and Wildlife Laboratory, Anchorage, Alaska 99503, personal communication, 1978), the western limit of the monk seal range, and caliciviruses have been isolated repeatedly from nursing and weaned elephant seals along the southern California coast (A.W. Smith, Naval Biosciences Laboratory, Oakland, California 94625, personal communication, 1978, 1979). Although there is no evidence to suggest that the recent die-off was in any way related to the presence of caliciviruses, it should be remembered that these agents have been associated with a vesicular disease and reproductive failure in California sea lions, *Zalophus californianus*, northern fur seals, *Callorhinus ursinus*, and domestic swine and cats.

Parasite ova found in the stool of the 10 young live seals at Laysan Island are described in Table 2. The following flatworm ova were recovered from the gastrointestinal tract of the adult (MS-11-78) which died at Laysan Island: *Corynosoma rauschi*, *Contracaecum turgidum*, *Diphyllobothrium cameroni*, *D. elegans*, and *D. hians*. *Contracaecum turgidum*, *Corynosoma rauschi* and *D. hians* were found in the stomach and intestines of MS-12-78 at French Frigate Shoals. These same parasite species were represented in many of the 13 animals which died at Laysan Island between 1 March and 1 May 1978.

All of the animals from which the tissue sets were collected, including the two examined by the authors, were cachetic and severely emaciated. Common findings in these 15 animals included: heart, lack of adipose tissue on the epicardium surface; liver, centralobular congestion, with foci of centralobular necrosis; lungs, congestion and alveolar hemorrhage in about half of the seals; spleen and lymph nodes, little or no evidence of lymphopoietic activity; testes, no evidence of spermatogenesis in males estimated to be subadult to adult; and, gastrointestinal tract, numerous foci of ulceration (many were actively hemorrhaging) with nematodes embedded deep into the stomach wall in all animals and many had additional intestinal lesions from cestodes, similarly embedded in the mucosa.

It is important to note that in December 1978, two additional monk seals were found dead at Laysan Island (B.W. Johnson and P.A. Johnson, personal communication, 1978) in an emaciated condition resembling that seen in April and May; however, these seals, on examination, had very light gastric nematode infestations and only minor ulceration at the phylorus.

TABLE 2. PARASITE OVA IN STOOL OF YOUNG LAYSAN MONK SEALS, 1978

Monk Seal	Cestode Ova*	Capillorid Type Ova*
MS-01	M	--
MS-02	H	L
MS-03	H	--
MS-04	M	L
MS-05	N.D.	N.D.
MS-06	N.D.	N.D.
MS-07	N.D.	N.D.
MS-08	H	--
MS-09	H	--
MS-10	H	--

*Number of ova in 400 power microscope field: L (light) = <25, M (moderate) = 25 to 75, H (heavy) = >75, N.D. = not determined

The extensive pathology caused by parasites, even though common to all of the monk seals which were necropsied during the period of high mortality in the spring, may be the result of seasonal fluctuations in gastric nematode parasite load and not, necessarily, a major factor in the spring 1978 mortality. Gastric nematode infestations, many with associated ulcerations, are relatively common in pinnipeds and since gastrointestinal tracts of only emaciated animals were examined, it is not possible to know the associated parasite pathology in the "normal" population. Table 2, however, indicates many of the apparently normal seals were carrying heavy cestode loads.

No dioxan was detected in the liver samples tested. Ciguatoxin and maitotoxin bioassay analyses of liver tissues from the adult which died at Laysan Island (MS-11-78) and the juvenile at French Frigate Shoals (MS-12-78) were positive. Estimated levels were 30 to 50 times that found in the liver of a control monk seal which had been maintained in captivity for 15 years. Radioimmunoassay for ciguatoxin in the same tissues revealed the liver of MS-11-78 to be about 25% above the control liver, while MS-12-78 was 9% below the control. Subsequent studies, the results of which will be published elsewhere, have shown that eels (known to be a part of the monk seal diet), collected near the islands on which the monk seals haul out, can debilitate and kill northern elephant seals after consumption of as little as 1.7% of the animal's body weight (DeLong and Gilmartin, in preparation).

The parasite associated pathology and the presence of ciguatoxin in the animals were the major findings which might account for this die-off of monk seals. Lack of any pathology in any organ systems (other than gastrointestinal) may discount any infectious disease processes of viral or bacterial origin.

Further study is needed to assess the impact of heavy gastrointestinal parasitism on pinnipeds relative to their general health and ability to feed and otherwise function normally. The signs displayed by the dying monk seals observed at Laysan Island are not inconsistent with what might be expected if the parasites were responsible, but they also could have been caused by the ciguatera syndrome. Ciguatera, which will kill a phocid seal, is known to be present in tropical reef environments and is present in the island chain in at least one of the monk seals' food fish. Continued disease monitoring of the seal population and experimental work in parasitology and ciguatera toxicology will be necessary to resolve the impact of these on the Hawaiian monk seal.

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EXPLORATORY FISHING ON THE HANCOCK SEAMOUNTS BY THE *TOWNSEND CROMWELL*, 1976-79

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ABSTRACT

Under authority of the U.S. Fishery Conservation and Management Act (FCMA) of 1976, which extended jurisdiction over fishery resources within 200 miles of the nation's coastline, the National Marine Fisheries Service initiated a program to collect catch and effort data and biological information on the pelagic armorhead, *Pentaceros richardsoni*, and alfonsin, *Beryx splendens*, at Hancock Seamounts which fall within the Fishery Conservation Zone. Data were collected from three sources--research cruises of the NOAA ship *Townsend Cromwell*, fishing trips of Japanese commercial vessels carrying U.S. observers, and fishing trips of Japanese commercial vessels fishing in 1969-76 prior to the enactment of the FCMA. The preliminary results of this study showed that 77% of the *Cromwell*'s catch in 1979 consisted of armorheads, that night trawling was significantly more productive than day trawling, and that 95% of the armorhead were the so-called "lean" type. Experimental handline fishing over the seamounts revealed that in addition to armorheads and alfonsins, the Japanese mackerel, *Scomber japonicus*, also appeared to be in relatively good numbers.

Hancock Seamounts
Pentaceros richardsoni
Beryx splendons
bottom trawling
handline fishing

INTRODUCTION

The central North Pacific seamounts extend to the northwest from the northern end of the Hawaiian ridge towards the Emperor Seamount chain. Southeast Hancock and Northwest Hancock are the most southeasterly of this group (Figure 1), respectively located 300 and 367 km (162 and 198 nmi) to the northwest of Kure.

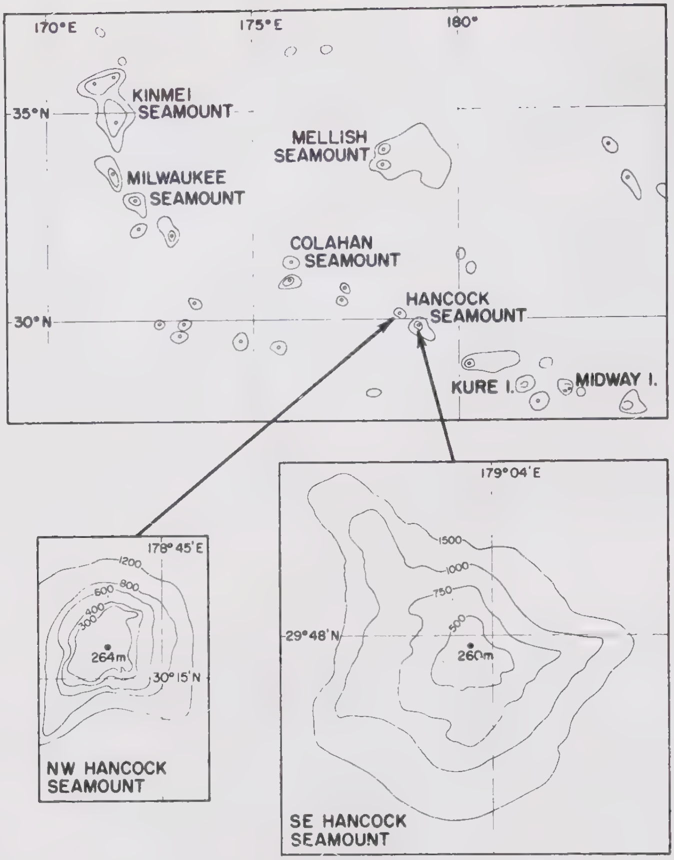
170°E
175°E
180°
35°N
30°N
KINMEI SEAMOUNT
MELLISH SEAMOUNT
MILWAUKEE SEAMOUNT
COLAHAN SEAMOUNT
HANCOCK SEAMOUNT
KURE I.
MIDWAY I.
178°45'E
1200
800
600
400
300
264m
30°15'N
NW HANCOCK SEAMOUNT
179°04'E
1500
1000
750
500
29°48'N
260m
SE HANCOCK SEAMOUNT

Figure 1. The location of Hancock Seamounts in relation to Midway and Kure and other North Pacific seamounts, and their depth configurations

Until quite recently interest in this group of seamounts, as in others, has primarily been geological, and almost nothing was known about their biological resources. However in 1967 a Russian trawler discovered the occurrence of pelagic armorhead, Pentaceros richardsoni, and alfonsin, Beryx splendens, on the seamounts northwest of the Hawaiian chain (Sakiura, 1972) and a fishery was born. In 1969 Japanese trawlers, which had been diverted from the Bering Sea fishing grounds, joined the Soviets in exploiting the new fishery.

Sakiura (1972) in his translation of a Russian paper, reported that commercial trawlers of the U.S.S.R. harvested approximately 133,400 metric tons (MT) of pelagic armorhead during 1969-70. Except for this remarkably high estimate of early catches on the then virgin grounds, no information on subsequent Soviet fishing is available.

Pelagic armorhead make up approximately 90% of the Japanese trawl catches from the seamounts with alfonsin and rockfish, Sebastes matsubari, constituting most of the remainder of the commercially valuable part of the catch.

In the Japanese bottom longline fishery the prime target species is alfonsin, followed by Sebastes sp. and Epinephelus sp.

For the Japanese, during the early years (1969 to 1971) of the seamount trawl fishery, there was considerable variation in both catch and effort. From 1972 to 1976 the catch of pelagic armorhead stabilized at 20,000 to 30,000 MT/yr. However, as fishing effort increased, catch per unit effort (CPUE) decreased each year, with CPUEs in metric tons per hour of trawling of approximately 60 in 1972, 34 in 1973, 22 in 1974, 14 in 1975, and 10 in 1976 (Sasaki, 1978). These figures include all Japanese commercial trawling in the central North Pacific seamount fishery. Available information indicate that the Hancocks were very productive grounds for pelagic armorhead, with catch rates reaching 83 MT/h in 1972, 40 MT/h in 1973, and 23 MT/h in 1974, 16 MT/h in 1975, and 11 MT/h in 1976 (Japan Marine Fishery Resource Research Center, 1973; Takahashi and Sasaki, 1977).

Since the Japanese bottom longline fishery for alfonsin, which began on the Milwaukee Banks around 1972, is a so-called "open fishery," requiring no permits or licenses in Japan, virtually nothing is known about the activity of the Japanese longline vessels. However, fragmentary reports indicate that the CPUE for longline-caught alfonsin was also declining through 1975 (Suisan Sekai, 1976; Sasaki, 1978).

On March 1, 1977, the United States, under authority of the Fishery Conservation and Management Act (FCMA) of 1976, extended its jurisdiction over fishery resources to all the area within 200 miles of the nation's coastline. The 200-mile Fishery Conservation Zone (FCZ) around the Hawaiian Archipelago included all of Southeast Hancock. The 200-mile line actually crosses Northwest Hancock, but apparently all of the relatively shallow trawlable ground on this seamount also falls within the FCZ.

In January 1977 the National Marine Fisheries Service (NMFS) Southwest Region published an environmental impact statement and Preliminary Fishery Management Plan which in essence limited fishing for pelagic armorheads and alfonsins within the FCZ by foreign vessels to 50 vessel-days per year each of trawling and bottom longlining. The annual quota by foreign vessels of pelagic armorheads and alfonsins was set not to exceed 2,000 MT/yr of either species or of the combined species.

Under the FCMA, Japan and the U.S.S.R. were each allocated 1,000 MT of seamount groundfish for 1977. No Japanese vessels fished on the Hancock Seamounts in 1977. In May 1977 a Soviet trawler, the Ekvator, was apprehended and cited by the U.S. Coast Guard for trawling in the Hancock area contrary to regulations defined in the FCMA. This vessel had taken 22 MT of pelagic armorhead within the FCZ.

In 1978 the Ryuyo Maru No. 2 was the only foreign vessel to fish the Hancock Seamounts. It was chartered by the Japan Marine Fishery Resource Research Center (JAMARC), and was accompanied by a NMFS observer (Kazama, 1978). In 1979 the sole foreign vessel to fish on the Hancocks was the commercial Japanese trawler, Aso Maru, also accompanied by a NMFS observer (Evering, 1979).

No U.S. commercial fishing vessels presently fish or have ever fished on the north central Pacific seamounts.

The National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory, conducted only intermittent resource surveys of the Hancock Seamounts. The data presented in this report are based on five exploratory fishing surveys during Townsend Cromwell cruises 76-06, October 1976; 77-02, May 1977; 78-01, February 1978; 78-03, September 1978; and 79-02, May 1979.

METHODS

Bottom fishing was conducted by stern trawling and hook-and-line fishing.

During the first cruise in 1976 the net used was a high opening Norwegian fish trawl with a 20-m headrope and a 25-m footrope. On the subsequent cruises, a larger "Noreastern" fish trawl with a 27-m headrope and a 32-m footrope was used with a pair of 1.8 x 2.7 steel V-type doors.

On the first two cruises (76-06 and 77-02) only blind tows, without the aid of a net sonde, were conducted. On the last three cruises, a "Noreastern" trawl was used with a Furuno 400 Mark II[1] net recorder (net sonde).

Handline fishing on the seamounts was conducted with 20-hook gear using cut squid as bait. During the first two cruises lines were manually handled. On subsequent cruises hydraulic gurdies were employed.

RESULTS

Trawling

During the five cruises, nine successful trawl tows (net was on the bottom), totaling 137 minutes of fishing time, were made on Northwest Hancock and three successful tows, totaling 77 minutes, were made on Southeast Hancock (Table 1). On cruise 78-01, the net sonde was used for the first time, however, it was malfunctioning and none of the four trawls made on Southeast Hancock were on the bottom, resulting in zero catch. Table 1 lists weight and the total catch of fish species taken in the 12 successful trawls. Table 2 gives pertinent information for each trawl and lists the dominant species taken on each station.

As noted earlier, during the first two cruises trawling was conducted without a net sonde. Although a net sonde was used on cruise 78-03, it was not until the last cruise that the vessel personnel had acquired a reasonable degree of expertise in the use of the equipment. This may be one of the factors responsible for the remarkably larger catches of armorhead on cruise 79-02 compared to earlier cruises. Another is that cruise

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1. FISHES CAUGHT TRAWLING ON HANCOCK SEAMOUNTS BY THE *TOWNSEND CROMWELL* IN ORDER OF THEIR ABUNDANCE IN THE HAULS BY WEIGHT

Fish	Number	Weight (kg)
Pentaceros richardsoni	2,579	975
Promethichthys prometheus	282	172
Zenopsis nebulosus	188	61
Squalus fernandinus	53	60
Beryx splendens	304	49
Ariomma lurida	134	31
Conger sp.	11	21
Antigonia steindachneri	137	7
Physiculus edelmanni	40	5
Polymixia nobilis	14	4
Emmelichthys sp.	17	2.7
Priacanthus boops	13	2.6
Diaphus trachops	145	2.6
Brotulidae	36	2.5
Polymixia japonica	29	2.4
Mytophum nitidulum	138	1.7
Hyperoglyphe japonica	2	1.3
Isistius brasiliensis	4	1.0
Sternoptychidae	2	<1
Antigonia eos	26	<1
Macrorhamphosus scolopax	8	<1
Chascanopsetta prorigera	3	<1
Parabothus coarctatus	10	<1
Argentia sp.	32	<1
Lophiomus miacanthus	4	<1
Tosanoides filamentosus	1	<1
Bothidae	6	<1
Centroscyllium nigrum	3	<1
Beryx decadactalys	1	<1
Hoplichthys sp.	1	<1
Pseudanthias kelloggi	2	<1
Rhynchocymba nystromi nystromi	4	<1
Astronesthus lucifer	1	<1
Argyropelecus aculeatus	2	<1
Etmopterus villosus	3	<1
Physiculus grinnelli	1	<1
Argyripnus atlanticus	1	<1
Parapercis roseoviridis	2	<1
Peristedion engyceros	1	<1

TABLE 2. DOMINANT SPECIES (BY WEIGHT) TAKEN IN 12 TRAWLS ON THE HANCOCK SEAMOUNTS ON *TOWNSEND CROMWELL* CRUISES

Dominant Species in Haul (Weight)	No. Fish	Weight (kg)	Area SE - NW Hancock	Date	Local Time	Bottom Depth (fm)	Surface Temp. °C	Bottom Temp. °c	Fishing Time (min)	Cruise No.	Station No.	Total Catch (kg)	Percentage of *P. richardsoni* in catch
P. richardsoni	34	21.9	SE	10/24/76	2133	145-160	25.2	13.5	19	76-06	49	29.7	74
B. splendens	3	3.6											
M. nitidulum	125	1.6											
P. richardsoni	64	21.0	SE	5/2/77	0835	144-170	21.5	12.6	20	77-02	52	68.0	31
A. lurida	134	30.5											
S. fernandinus	6	5.0											
Z. nebulosa	14	4.0											
Emmelichthys sp.	16	2.7											
Z. nebulosa	11	3.0	NW	9/9/78	1324	155-165	26.6	12.0	10	78-03	31	3.2	0
B. splendens	1	0.1											
A. eos	5	0.1											
P. richardsoni	118	59.5	NW	9/10/78	2150	150-165	26.6	12.0	15	78-03	33	95.0	28
P. prometheus	22	25.1											
Z. nebulosa	61	23.8											
S. fernandinus	4	3.6											
A. eos	37	2.7											
B. splendens	44	2.3											
P. richardsoni	32	71.2	NW	9/10/78	0925	155-165	26.6	12.0	23	78-03	34(1)	18.7	60
Z. nebulosa	24	6.9											
H. japonica	5	0.3											
A. eos	10	0.3											
B. splendens	99	18.1	NW	9/10/78	1115	155-165	26.6	12.0	20	78-03	34(2)	37.2	25
Z. nebulosa	36	9.9											
P. richardsoni	26	9.2											
A. eos	9	0.3											
P. richardsoni	31	10.5	NW	5/4/79	1405	147-149	19.9	15.0	14	79-02	26	14.7	71
Z. nebulosa	7	2.0											
A. steindachneri	17	0.5											
P. richardsoni	10	3.5	NW	5/5/79	1000	144-150	20.9	14.9	17	79-02	31	6.9	51
Z. nebulosa	12	2.8											
A. steindachneri	11	0.3											
P. richardsoni	270	93.6	NW	5/5/79	2116	144	20.4	14.2	14	79-02	33	113.8	82
P. prometheus	28	10.5											
B. splendens	32	4.7											
D. trachops	145	2.6											
P. richardsoni	553	208.0	NW	5/5/79	2320	141	20.5	14.2	13	79-02	34	228.7	91
S. fernandinus	4	8.5											
P. prometheus	15	7.0											
B. splendens	14	1.4											
P. prometheus	225	132.9	NW	5/6/79	0155	144	20.5	14.4	11	79-02	35	165.8	15
P. richardsoni	70	25.1											
B. splendens	50	7.8											
P. richardsoni	1,373	546.0	SE	5/6/79	2100	140	19.9	14.8	38	79-02	37	614.9	89
S. fernandinus	39	43.5											
B. splendens	60	7.4											
Z. nebulosa	31	6.9											

78-03 followed the fishing trip of the Japanese trawler *Ryuyo Maru No. 2* at Hancock whereas on cruise 79-02 the *Cromwell* preceded the Japanese trawler *Aso Maru*. On cruise 79-02 the mean catch per hour was 642 kg total and 497 kg for armorhead, whereas for the three other cruises combined the mean catch per hour was 108 kg total and 62 kg for armorhead. This heterogeneity in such limited data precludes any extensive analysis. From Table 2 it is clear that, in general, the same species dominated the catches, and that our catch results, in agreement with those of the Japanese and Soviets, indicate that evening and night trawls are far more productive than day trawls. The mean night catch per hour was 680 kg total and 520 kg armorhead compared to mean day catch rates of 86 kg total and 38 kg for armorhead.

For cruise 79-02 the mean length of armorhead was 25.5 cm for both males and females, and 95% of the fish were the so-called "lean" type. This is the same proportion of lean fish reported for the *Aso Maru*. It is of some interest to note that only on the best hauls, during cruise 79-02 (stations 33, 34, and 37), did the percentage of armorhead in the catch approach that reported for Japanese trawlers (Sasaki, 1978).

Handlining

Table 3 summarizes the handlining conducted on the seamounts. Line hours fished totaled 24 at seven stations on Southeast Hancock and 28 at six stations on Northwest Hancock. Armorhead were most abundant with a mean catch for all fishing stations of 1.7 kg/line-hour. Although alfonsins were taken in small numbers on four stations, the overall mean catch of 0.2 kg/line-hour was very low. The largest catch, 37.4 kg/line-hour of Japanese mackerel, *Scomber japonicus*, was made on Southeast Hancock, during *Townsend Cromwell*'s first visit to the seamounts.

DISCUSSION AND CONCLUSIONS

The *Townsend Cromwell*'s fishing activity on the Hancock Seamounts has provided much needed experience for NMFS scientific and vessel personnel. However, the data we have collected are certainly insufficient to allow even general speculation on the condition of the armorhead and alfonsin fishery on the Hancock Seamounts.

Subsequent to cessation of intensive foreign commercial fishing on the Hancocks, since the 1976 season, the only other data available on the fishing conditions in the area are from trawling operations of the *Ryuro Maru No. 2* in 1978 and the *Aso Maru* in 1979. The impression of the NMFS observers assigned to those vessels was that the Japanese considered fishing to be poor when compared to the conditions which prevailed during earlier years of the fishery.

Townsend Cromwell cruise 80-02 during April of 1980 will conduct the most intensive survey of the Hancock Seamounts and others in the vicinity of Kure and Midway Islands thus far attempted by NMFS. In addition to bottom fishing with trawl and handlines, we will utilize 100-hook bottom longline gear similar to that used in the Japanese alfonsin fisheries.

A U.S. domestic seamount fishery would seem unlikely in the near future. However, foreign interest in the Hancock Seamount grounds will probably continue.

To develop an acceptable fishery management plan, NMFS will require an adequate data base. Future plans at the Southwest Fisheries Center Honolulu Laboratory call for a comprehensive study of the Hancock Seamounts and other seamounts located within the Hawaiian Island FCZ.

SUMMARY

A study of fishery resources over Hancock Seamounts, which are located within the FCZ of the Hawaiian Archipelago, was initiated in October 1976. Data collected aboard the *Townsend Cromwell* were in general agreement with Japanese fishing results which indicated that catch rates were significantly higher at night rather than during daytime and that a large proportion of the catch at Hancock Seamounts consisted of pelagic armorhead, *Pentaceros richardsoni*, most of which were the so-called "lean" type. The balance of the catch consisted of alfonsin, *Beryx splendens*. Handline fishing also produced relatively good numbers of Japanese mackerel, *Scomber japonicus*. Future research needs include

TABLE 3. HANDLINE CATCHES ON THE HANCOCK SEAMOUNTS ON *TOWNSEND CROMWELL* CRUISES

Species	No. Fish	Weight (kg)	Area SE - NW Hancock	Date	Fishing Time (Local)	Cruise No.	Station No.	Catch Per Line-Hour (kg)
Scomber japonicus	28	43.6	SE	10/29/76	1740-1815	76-06	47	37.4
Hyperoglyphe japonica	1	6.4						5.5
Pentaceros richardsoni	2	1.4						1.2
Decapterus russellii	1	1.2						1.0
Squalus fernandinus	1	0.7						0.6
Beryx splendens	1	0.9	SE	10/29/76	1822-1930	76-06	48	1.0
Hyperoglyphe japonica	2	4.2	SE	5/25/77	1815-2145	77-02	50	0.6
Squalus fernandinus	3	3.3						0.5
Pentaceros richardsoni	6	2.9						0.4
Beryx splendens	1	0.8						0.1
Squalus fernandinus	12	14.1	SE	2/10/78	0950-1135	78-01	60	4.0
Scomber japonicus	11	13.6						3.9
Decapterus russellii	4	4.5						1.2
Pentaceros richardsoni	7	3.2						1.0
Squalus fernandinus	4	7.1	SE	2/11/78	0820-0905	78-01	67	4.7
Pentaceros richardsoni	8	2.6						1.7
Decapterus russellii	1	0.9						0.6
Pentaceros richardsoni	60	21.2	SE	2/11/78	1115-1435	78-01	68	3.2
Squalus fernandinus	13	17.4						2.6
Hyperoglyphe japonica	1	2.0						0.1
Scomber japonicus	1	0.5						0.03
Hyperoglyphe japonica	1	2.2	NW	9/7/78	1736-2107	78-03	26	0.3
Beryx splendens	1	0.9						0.15
Pentaceros richardsoni	2	0.7						0.14

TABLE 3. HANDLINE CATCHES ON THE HANCOCK SEAMOUNTS ON *TOWNSEND CROMWELL* CRUISES (Continued)

Species	No. Fish	Weight (kg)	Area SE - NW Hancock	Date	Fishing Time (Local)	Cruise No.	Station No.	Catch Per Line-Hour (kg)
Pentaceros richardsoni	9	3.8	NW	9/8/78	0900-1133	78-03	28	1.2
Scomber japonicus	1	1.2						0.4
Hyperoglyphe japonica	1	1.2						0.4
Decapterus russellii	1	1.2						0.4
Pseudanthias	1	0.2						0.1
Hyperoglyphe japonica	7	12.4	NW	9/9/78	1746-2011	78-03	32	2.6
Pentaceros richardsoni	5	1.9						0.4
Scomber japonicus	1	1.4						0.3
Squalus fernandinus	1	1.2						0.2
Pentaceros richardsoni	34	13.2	NW	10/2/79	1647-2012	79-02	28	4.7
Beryx splendens	1	0.8						0.3
Pentaceros richardsoni	23	10.0	NW	10/2/79	0519-1842	79-02	30	1.5
Beryx splendens	9	7.8						1.2
Hyperoglyphe japonica	2	3.8						0.6
Pentaceros richardsoni	51	25.37	NW	10/2/79	1818-1957	79-02	32	7.7
Hyperoglyphe japonica	2	3.9						0.6
Pentaceros richardsoni	10	3.8	SE	10/3/79	1910-2005	79-02	36	1.3

monitoring of the stock at Hancock Seamounts and additional surveys of other seamounts in the vicinity of Kure and Midway. Collection of biological and morphometric data will be continued.

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Cooperative Survey of Rockfish and Whiting Resources Off California, Washington, and Oregon, 1977: Introduction

Papers presented at a symposium in Seattle, Wash., 6-7 July 1978

DONALD R. GUNDERSON and WILLIAM H. LENARZ, Editors

Pacific coast rockfish (genera *Sebastes* and *Sebastolobus*) dominate commercial bottomfish landings in California, Oregon, and Washington. In 1977, 22,900 metric tons (t) of rockfish were landed by commercial fishermen, making up 38 percent of the total bottomfish landings. In addition, at least 2,600 t of rockfish (excluding Puget Sound, Wash., catches) were caught by recreational fishermen during the same year.

The Pacific ocean perch, *Sebastes alutus*, is the most abundant rockfish in the eastern North Pacific Ocean; the species was studied extensively after its rapid and drastic decline due to overexploitation by foreign trawlers in the 1960's. In contrast, only limited research was carried out on rockfish other than Pacific ocean perch, and when the U.S. Fishery Conservation and Management Act of 1976 was enacted, information needed to manage all of the rockfish resource was quite sketchy. Shortcomings in existing knowledge of biology and stock conditions for all rockfish species made it apparent that an intensive survey of these resources would be desirable.

A 3-day workshop was convened in January 1976 at the National Marine Fisheries Service's Northwest and Alaska Fisheries Center (NWAFC), Seattle, Wash., to assess the extent of information on the resource. The workshop was attended by representatives of the California Department of Fish and Game, National Marine Fisheries Service, Oregon Department of Fish and Wildlife, Oregon State University, Washington State Department of Fisheries, and the University of Washington.

A rockfish survey coordinating committee was established at this meeting to develop a cooperative pilot survey in 1976 and a coastwide survey of rockfish and Pacific whiting, *Merluccius productus*, resources in 1977. Meetings between representatives of NMFS and the Polish Sea Fisheries Institute (Gdynia, Poland) in 1977 served to coordinate Polish research efforts with those of the other agencies involved in the rockfish surveys.

Following completion of the 1977 survey, the participants analyzed data on specific areas of interest and responsibility, summarized the results, and prepared reports for a symposium held in July 1978 in Seattle. The papers in this issue, 42(3-4), of *Marine Fisheries Review* were among those presented at the symposium. Results of oceanographic studies carried out during the survey were also presented at the symposium and are available in an article by Ingraham and Love (1978).

The information included in this collection of papers substantially increases our knowledge of Pacific rockfish resources and suggests several important avenues of future research for these species. The magnitude and nature of a latent resource of potential importance (shortbelly rockfish, *Sebastes jordani*) is outlined. Also provided is information on the abundance, age composition, growth, fecundity, and size at maturity for those species that are important commercially: Pacific ocean perch; bocaccio, *Sebastes paucispinis*; chilipepper, *S. goodei*; yellowtail rockfish, *S. flavidus*; and canary rockfish, *S. pinniger*. Patterns in age composition indicated that significant northward migrations of shortbelly rockfish, chilipepper, bocaccio, and yellowtail rockfish occur over the course of their juvenile and adult lives, and a similar phenomenon is suspected in the case of splitnose rockfish, *S. diploproa*, and Pacific ocean perch.

Many rockfish larvae appear to spend several months in the pelagic zone, and this migration is possibly an adaptation to counterbalance the southerly transport that characterizes this region (particularly between Cape Blanco and Point Conception) during much of the year (Bakun et al., 1974). The age composition data together with the results of biochemical genetic studies that were carried out in conjunction with the survey suggest that a much higher degree of intermingling of Pacific coast rockfish stocks takes place than was previously thought to be the case.

Survey results for Pacific whiting were equally useful and supplemented existing knowledge of this important resource considerably. Biomass estimates indicated that the abundance of Pacific whiting increased sharply between 1975 and 1977, due partly to the recruitment of a strong 1973 year class to the stock. This information proved useful in evaluating the status of the Pacific whiting resource and contributed to the decision to increase the Total Allowable Catch for 1979.

The editors are grateful to Roger Pearson, Samuel Waterman, and Rae Mitsuoka of the NWAFC for their assistance in editing the papers in this collection. The assistance of James Peacock and his graphics unit at the laboratory is also gratefully acknowledged.

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THE STATUS OF SEABIRD RESEARCH IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

The five-year objectives of the U.S. Fish and Wildlife Service (FWS) are to enumerate Northwestern Hawaiian Islands seabird populations, inventory food utilized, locate major feeding areas, and determine consumptive rates. To date, preliminary assessment of populations has begun and a comprehensive food habits study is nearing completion. The 3,000 food samples from 18 seabird species analyzed thus far indicate that most birds feed opportunistically on shoaling fish and squid. The fish families Exocoetidae, Mullidae, Carangidae, Synodontidae, Dussumieriidae, Coryphaenidae, Molidae, and Holocentridae and the squid family Ommastrephidae appear to be especially important. Prey length data indicate that most terns and shearwaters feed on prey species in the 2 to 8 cm range and that boobies feed in the 10 to 20 cm range. An encouraging feasibility study using radiotracking with the brown noddy on Oahu resulted in a technique to locate feeding areas. Future objectives include completion of food studies and refinements of population estimation techniques. Information gaps still include location of feeding areas and knowledge of consumptive rates of seabirds. We need a better understanding of life histories, age structure, and annual production of important prey items including Ommastrephidae, Exocoetidae, Mullidae, and Synodontidae.

Northwestern Hawaiian Islands
seabirds
feeding ecology

INTRODUCTION

Seabirds are a relatively poorly studied group of birds. They can be characterized as being relatively long-lived, displaying deferred maturity, reproducing slowly, and possessing salt excretion glands which enable them to drink salt water (Bourne, 1963; Lack, 1967). Most species spend most of their lives at sea, but the fact that they must return to land to breed emphasizes the fact that they are terrestrial expatriates. Hutchinson (1950) contends that seabirds perform an important function for reef communities by concentrating nutrients in a localized area.

Large portions of the worldwide breeding range of the black-footed albatross (Diomedea nigripes), Laysan albatross (D. immutabilis), Bonin petrel (Pterodroma hypoleuca), Christmas shearwater (Puffinus nativitatus), sooty storm-petrel (Oceanodroma tristrami), blue-gray noddy (Procelsterna cerulea), and gray-backed tern (Sterna lunata) are within the Northwestern Hawaiian Islands (NWHI). Additionally 11 breeding species occur in the archipelago with total numbers of seabirds being estimated at 10 million birds. Seabird populations have plummetted when fisheries directly competed with birds for the same prey species in Peru (Idyll, 1973), South Africa and Southwest Africa (Crawford and Shelton, 1978), and possibly California (Ainley and Lewis, 1974). Recent fishery-seabird models indicate that birds may be unable to produce young if forage fish fall to 70% of virgin levels (MacCall, 1980). Tropical seabirds generally feed at the surface, or in the case of some birds of the order Pelicaniformes, within the first few meters. Ashmole and Ashmole (1967) contend that large predatory fish, especially scombrids, are important because they drive prey to the surface and make them available to the birds.

The internationally recognized importance of the NWHI seabird resource and the potential for adverse impacts from improperly managed fisheries in other parts of the world prompted the U.S. Fish and Wildlife Service to agree to enumerate NWHI seabird populations, inventory food utilized, locate major feeding areas, and determine consumptive rates. Crawford and Shelton (1978) point out, "The interrelationships of pelagic fishery and seabird populations signify the overriding importance of sound fishery management for other ecosystem components."

METHODS

The remoteness of the Nihoa to Kure study area has made access a major problem. Cruises on the R/V Townsend Cromwell, military air command flights to Midway, U.S. Coast Guard flights to Kure, and recent FWS involvement on Tern Island have provided sporadic opportunities to study the marine bird resources. In addition, field camps on Laysan Island from March to August in 1979 and 1980 have provided an opportunity to intensively follow reproductive biology, collect monthly food samples, and make detailed population estimates.

The variety of studies carried out to date precludes a detailed description of techniques and methods. Population assessments have been made with several techniques including direct counts and stratified random sampling. All food samples have been collected on the islands by utilizing generally non-lethal techniques. Approximately 100 Bonin petrels and Bulwer's petrels (Bulweria bulwerii) had to be sacrificed due to inabilities to induce regurgitation. In the laboratory, standard analytical techniques including sorting, identification, counting, volumizing, and measuring standard lengths were carried out (Ashmole and Ashmole, 1967). A telemetry project utilizing a 5.4 g transmitter package is described in detail in a forthcoming publication (Harrison and Stoneburner, in preparation). Reproductive biology, phenology, incubation shifts, and chick feeding intervals on Laysan Island were carried out with standard observation techniques, details of which will appear in forthcoming publications.

RESULTS AND DISCUSSION

It cannot be overemphasized that all statements and conclusions are tentative in this continuing study. Population estimates will be refined. Subtleties of feeding habits, including a somewhat different assessment of critical prey items, may well turn up when geographic and seasonal considerations are explored and the entire data base is accessible with automatic data processing techniques.

Populations

Seabird populations, like any real population of wild animals, are dynamic over time. This volatility is confounded by the fact that estimation techniques for some species are inherently imprecise. For example, cliff nesting blue-gray noddies and white terns (Gygis alba) on Nihoa and Necker are extremely difficult to census without low level aerial photographic capabilities. Sooty terns (Sterna fuscata) can be censused effectively only when incubating eggs. Adults scatter when an investigator enters a colony and once eggs hatch, chicks form crèches and density estimates become very imprecise. Given the propensity of this species to lay in sub-colonies over a 6 to 8-week period, an accurate census is only possible on a particular island by placing investigators at that location for at least a month during spring. Counts of roosting red-footed boobies (Sula sula) and black noddies (Anous tenuirostris) peak at approximately 0400 and censuses at other times of the day underestimate, often grossly, the true numbers of birds in a colony. On sandy atolls, nests or immobile young, e.g., albatross, are generally the easiest birds to census. This technique ignores large numbers of non-breeding birds which roost at a colony and forage in the vicinity. The attachment of pre-breeders and failed breeders to a colony is insufficiently understood for any species, but is necessary to determine true colony size and concomitant requirements for nearby marine food resources. Burrow nesting birds such as Bonin petrels and wedge-tailed shearwaters (Puffinus pacificus) also present special problems. Burrows can be easy to census if not crushed in the process, but may extend far underground and must be excavated in order to determine occupancy. It is a goal for the second half of this study to develop repeatable census methodologies for each species and habitat.

Table 1 presents our best present estimates of NWHI seabird populations and, additionally, mean adult weights for each species. Most bird weights are from Laysan Island and represent a sample size of approximately 50 adult weights per species. NWHI birds are generally heavier than birds from Christmas Island (Pacific Ocean) as reported by Ashmole and Ashmole

TABLE 1. POPULATION ESTIMATES AND ADULT WEIGHTS, NORTHWESTERN HAWAIIAN ISLANDS

	Nihoa	Necker	FFS	Gardner P.	Laysan	Lisianski	P & H	Midway	Kure	Mean weight (kg)
Black-footed Albatross	100	350	4,700	0	67,000	3,500	14,000	30,000	600	2.6
Laysan Albatross	tr	1,800	1,600	tr	550,000	8,000	45,000	500,000	2,400	2.4
Bonin Petrel	0	0	750	0	40,000	1,000,000	1,000	10,000	2,500	0.178
Bulwer's Petrel	250,000	200	500	tr	20,000	tr	tr	0	0	0.101
Wedge-tailed Shearwater	25,000	4,500	13,000	tr	1,000,000	500,000	26,500	20,000	1,500	0.390
Christmas Shearwater	800	0	tr	0	10,000	2,000	tr	100	tr	0.362
Sooty Storm-Petrel	tr	0	tr	0	2,500	0	7,500	0	0	0.084
Red-tailed Tropicbird	500	200	450	100	4,000	4,500	200	3,000	2,000	0.630
Masked Booby	350	500	1,200	800	2,000	1,200	600	20	100	2.2
Red-footed Booby	3,500	1,400	750	tr	2,500	3,000	200	1,000	600	1.1
Brown Booby	225	50	135	20	250	200	200	tr	100	1.3
Great Frigatebird	10,000	2,000	1,400	250	8,000	2,500	900	200	500	1.4
Sooty Tern	100,000	50,000	250,000	750	2,000,000	1,700,000	80,000	50,000	12,000	0.209
Gray-backed Tern	10,000	7,500	1,750	4,000	40,000	15,000	1,900	50	100	0.147
Blue-gray Noddy	2,500	2,500	tr	tr	tr	0	0	0	0	0.045
Brown Noddy	20,000	50,000	10,000	5,000	30,000	15,000	8,400	3,000	1,200	0.208
Black Noddy	2,000	1,000	11,000	400	5,000	5,000	4,300	5,000	2,000	0.107
White Tern	3,000	600	3,700	400	1,500	500	tr	6,000	tr	0.112

Note: tr = trace

(1967). Most population data are taken from the Atoll Research Bulletin series (Amerson, 1971; Amerson et al., 1974; Clapp, 1972; Clapp and Kridler, 1977; Clapp et al., 1977; Clapp and Wirtz, 1975; Ely and Clapp, 1973; Woodward, 1972). Our data have generally corroborated these estimates, but some changes will undoubtedly be forthcoming at the conclusion of this study. Revisions will reflect both genuine population changes and improved census technology. Estimates for Midway are our own. The largest concentrations of total birds and avian biomass occur on Laysan, Lisianski, and Midway. Midway's populations have been reduced by large scale habitat destruction and the introduction of *Rattus rattus*.

Food habits

Published accounts of feeding habits of tropical Pacific seabirds are limited. Ashmole and Ashmole (1967) provided data for 8 Christmas Island species (N = 800) and Schreiber and Hensley (1976) added 3 additional species for the same study area (N = 175). Table 2 lists samples collected by species and month through November 1979. This study is the most comprehensive tropical seabird work yet attempted. We expect to have

TABLE 2. TOTAL FOOD SAMPLES COLLECTED JANUARY THROUGH NOVEMBER 1979

SPECIES	MONTH												
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
Black-footed Albatross		41	12	28	42	3							126
Laysan Albatross	1	15	20	30	50	4	1						121
Bonin Petrel			5	36	51								92
Bulwer's Petrel					20	13	10	27					70
Wedge-tailed Shearwater					20	19	13	19	11	7	24		113
Christmas Shearwater			4	3	22	11	28	39	7				114
Sooty Storm-Petrel				7	1								8
Red-tailed Tropicbird		4			31	25	63	51	22	18			214
Masked Booby			11	16	42	10	12	33	2	3	15		144
Red-footed Booby	13	25	15	10	55	11	18	41	14	15	22		239
Brown Booby			4	10	25	8	20	27			21		115
Great Frigatebird		5	5	15	50	11	14	19	7	12	6		144
Sooty Tern			7	21	99	27	28	79	9				270
Gray-backed Tern			7	23	88	10	5	33					166
Blue-gray Noddy					42			1					43
Brown Noddy			14	14	69	4	70	61	3	9	1		245
Black Noddy	17	8	8	31	95	13	79	45	15	37			348
White Tern	4	6	2	4	34	23	18	61	28	11	5		196
TOTAL	35	104	114	248	836	192	379	536	118	112	94	0	2768

adequate sample sizes for all breeding NWHI species except for the sooty storm petrel, but the extremely digested sample condition makes it difficult to provide as much information as we had hoped for the Bulwer's petrel and the Bonin petrel. Data presented here are generally based on sample sizes of 30 to 50 per species and ignore potentially important differences in year, season, and location. We suspect seasonal changes may be very important. Continuing collections are designed to fill information gaps in geography and season.

NWHI seabirds feed on fish, squid, and arthropods. By volume, the blue-gray noddy feeds on the highest percentage of arthropods (25%), especially the insect _Halobates_ sp. Remaining species feed on no more than 8% of this phylum. Procellariiformes (albatross, shearwaters, and petrels) feed on slightly more fish than squid by volume, except for the Laysan albatross (70% squid) and the Bonin petrel (86% fish). The Pelicaniformes (boobies, tropicbirds, and frigatebird) feed almost exclusively on fish (>93% by volume) except for the red-footed booby (_Sula sula_) (Figure 1). Terns feed predominantly on fish with the

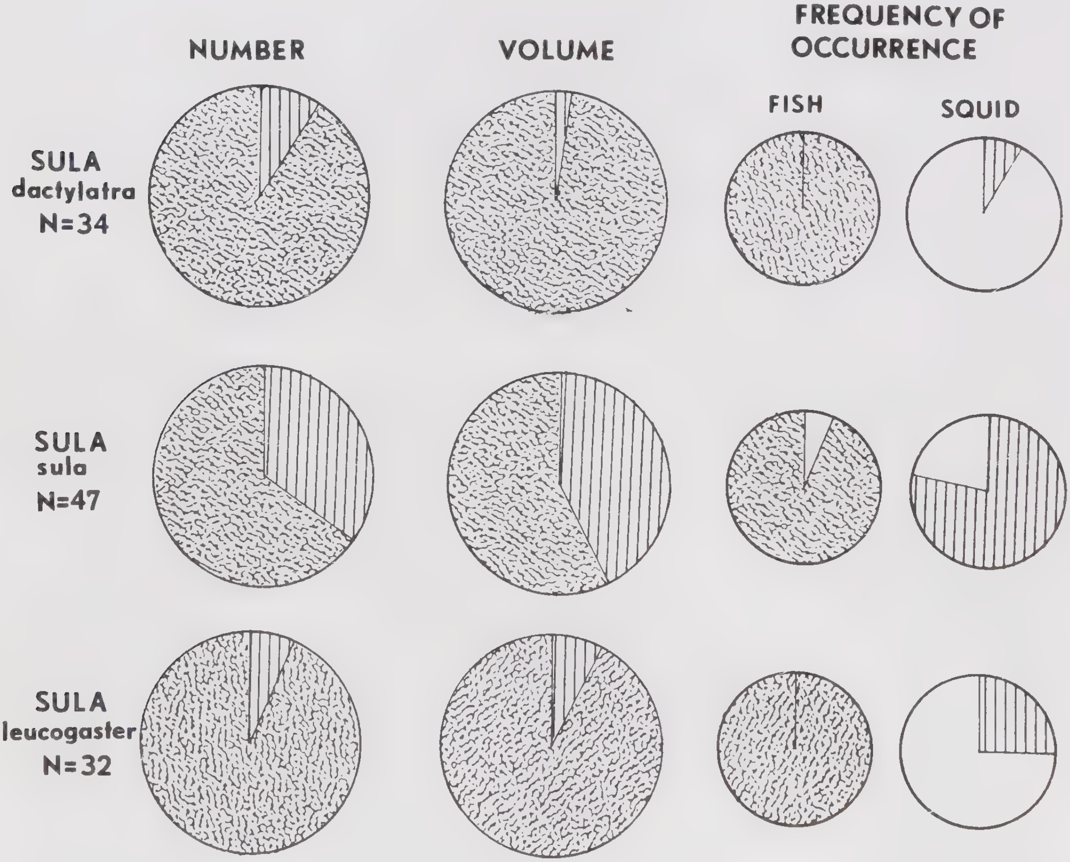


Figure 1. Relative importance of fish (stippled) and squid (lined) in diets of 3 boobies

exception of the sooty tern which feeds on 38% fish and 62% squid. Generally, NWHI seabirds eat a greater percentage of fish than species on Christmas Island.

Table 3 presents a ranking of important fish families in NWHI seabird diets. The rankings are obtained by use of the formula developed by Pinkas et al. (1971) in which

$$IRI = F(N+V)$$

where

IRI = Index of Relative Importance
F = Frequency of Occurrence
N = Numerical Percentage
V = Volumetric Percentage

We agree with their contention that while this equation may not be the last word in assessment of importance of prey items, it is superior to the exclusive use of any one of the commonly calculated statistics which comprise it. Rankings may change with time of year and locality, but at present we recognize the flying fish (Family Exocoetidae, especially *Exocoetus volitans* and *Cypselurus* spp.), the jacks (Family Carangidae, almost entirely *Decapterus* spp.), and the goatfish (Family Mullidae) to be of outstanding importance. Inshore feeding birds are marked with an asterisk in Table 3. Additional important forage families for this group are Dussumieriidae (*Spratelloides delicatulus*), Synodontidae (lizardfish), and Coryphaenidae (both species of mahimahi).

Squid are almost entirely of the family Ommastrephidae, and include the genera *Ommastrephes*, *Symplectoteuthis*, and *Hyaloteuthis*.

Figures 1, 2, and 3 portray feeding comparisons of three congeneric boobies, the masked booby (*Sula dactylatra*), the red-footed booby (*Sula sula*), and the brown booby (*Sula leucogaster*). These figures portray percentages of the major prey groups (number, volume, frequency of occurrence), comparative use of fish families, and comparative lengths of fish consumed. An upcoming monograph will display data for all species and compare localities and seasons where appropriate.

Seabird diets are complex and not easy to generalize in the NWHI. They feed opportunistically on surface shoaling fish and squid and occasionally supplement this diet with crustaceans and insects. They have evolved to utilize an assemblage of prey species, which may help to moderate the vicissitudes of the sub-tropical marine environment. The presence of mid-water fish such as lanternfish (Myctophidae) and hatchetfish (Sternoptychidae) suggest that some species feed nocturnally or crepuscularly, but direct observations are lacking except for sooty terns and wedge-tailed shearwaters (Gould, 1967). Many NWHI populations have apparently evolved breeding chronologies to take advantage of seasonally abundant fish larvae and juveniles of Mullidae, Synodontidae, and Holocentridae.

TABLE 3. RANKED IMPORTANCE OF FISH FAMILIES IN NWHI SEABIRD DIETS

Seabird	Carangidae	Coryphaenidae	Dussumieriidae	Engraulidae	Exocoetidae	Gempylidae	Holocentridae	Molidae	Monacanthidae	Mullidae	Myctophidae	Nomeidae	Ostraciontidae	Scombridae	Synodontidae
Black-footed Albatross					1										
Laysan Albatross					1			2							
Bonin Petrel										1	2				
Wedge-tailed Shearwater	3								2	1					
Christmas Shearwater	2				1					3					
Red-tailed Tropicbird	2	4			3			1							
Masked Booby	2				1									3	
Red-footed Booby	3			2	1										
Brown Booby *	2				1					3					
Great Frigatebird	2				1										
Sooty Tern	5				2	4	3			1					
Gray-backed Tern *	4		1		3					6		2	5		
Blue-gray Noddy *					3					1					2
Brown Noddy	3		6		7	5	4			1					2
Black Noddy *			4		2					1					3
White Tern *		3			2					1					

*Inshore feeding birds

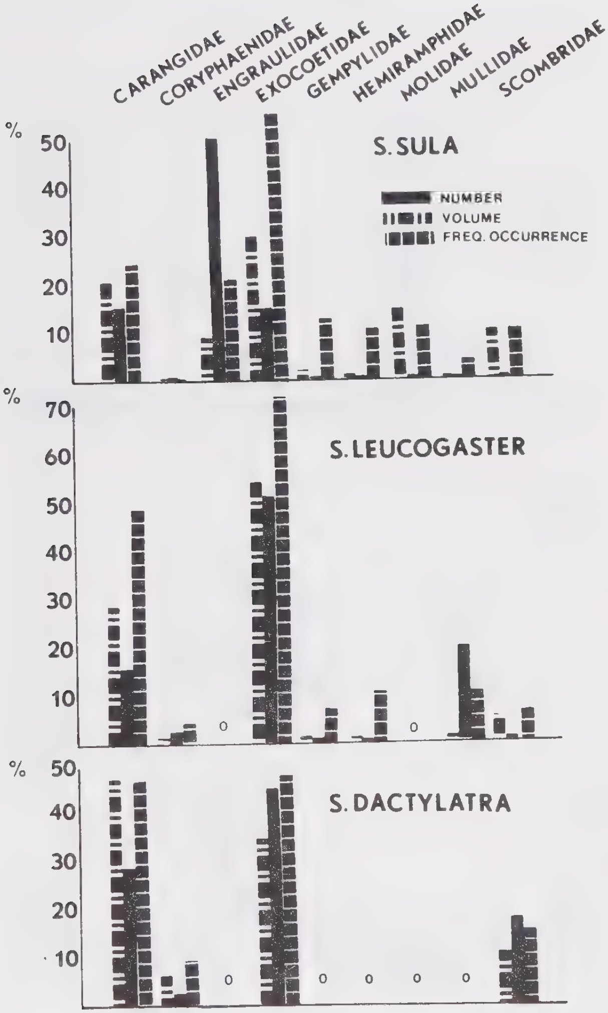


Figure 2. Comparison of fish families preyed on by three booby species

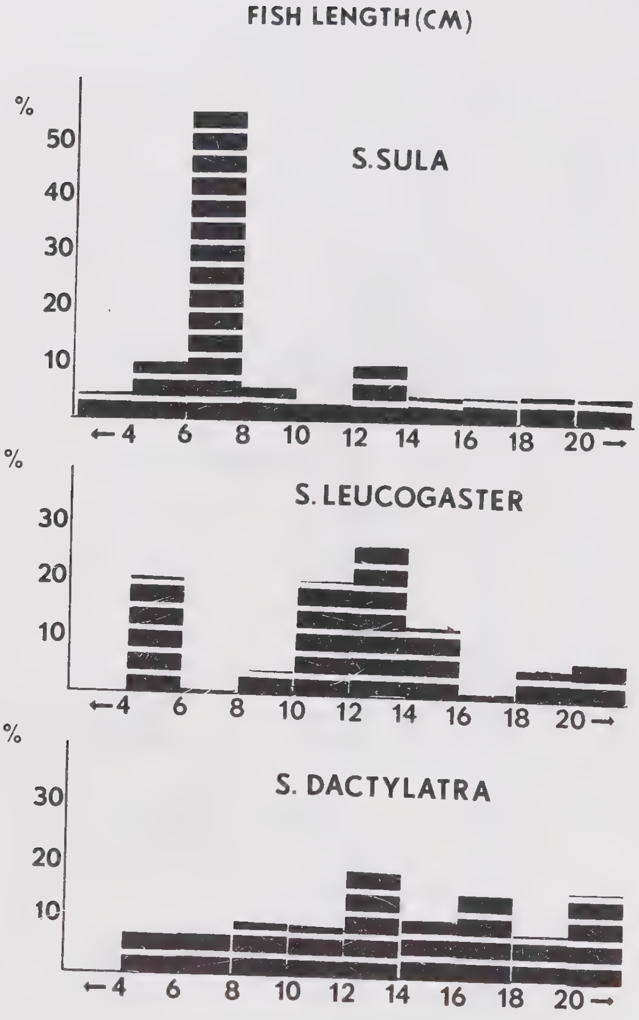


Figure 3. Comparison of fish lengths preyed on by three booby species

Feeding rates

We have no direct information concerning feeding rates. Table 1 lists the first published values for weights of NWHI seabirds. Our Laysan Island studies on growth rates of young, fledging times, and reproductive chronology could be used to determine consumptive rates and the amount of food necessary to raise young if some basic physiological data concerning energy metabolism were available.

Feeding areas

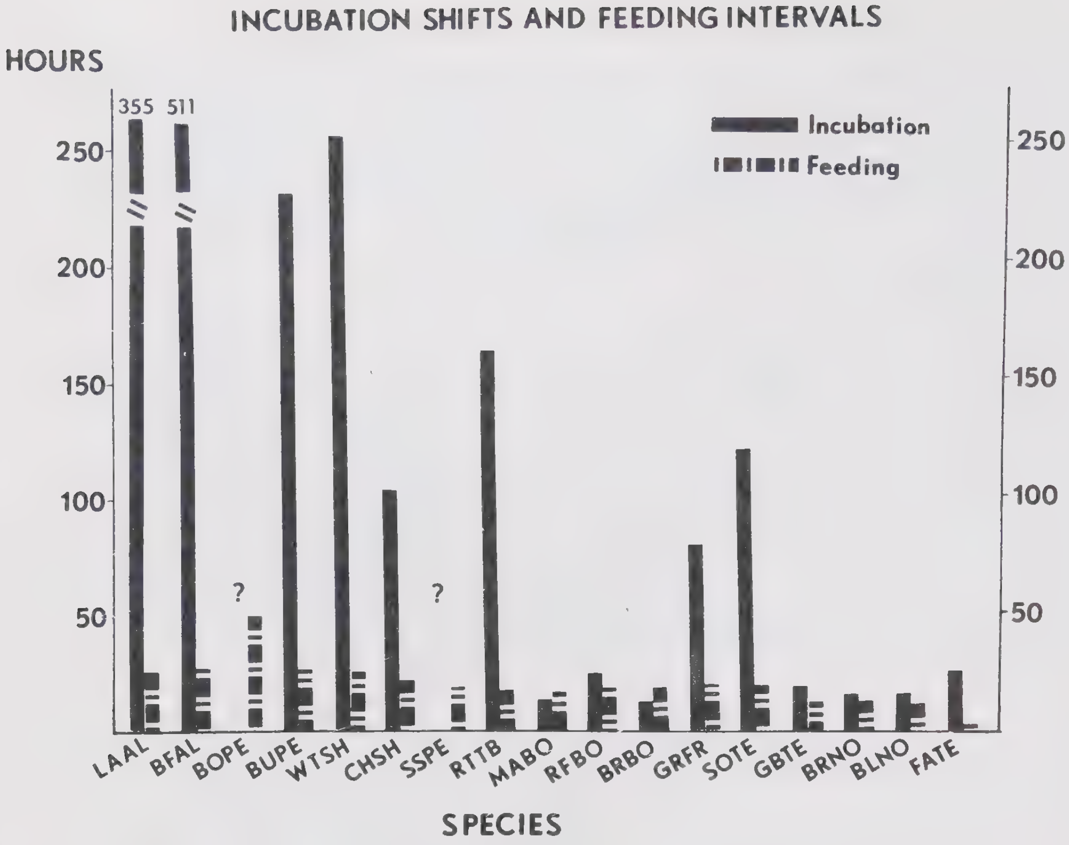
Bourne (1963) stated, "There is clearly a need for more direct observations of where and how birds feed at sea." This situation has not changed in almost two decades. Figure 4 depicts an indirect measure of feeding areas by portraying the lengths of time incubating adults are away at sea during one shift and length of time between feedings for growing chicks. If these times are a true reflection of feeding areas, a sharp contraction of feeding range occurs when the egg hatches. However, we do not necessaily accept the unproven hypothesis that there is a strong correlation between feeding distance and length of time an adult spends away from the colony. For example, two species with vastly different incubation intervals could be feeding in precisely the same area, but one may take longer to locate and obtain its prey.

A feasibility study of radiotracking the brown noddy (*Anous stolidus*) took place on Oahu in September 1979. Although the birds flew beyond our 16-km detection range and consequently we did not learn the precise feeding areas, two important points can be made from Figure 5. The first is that birds of this species do not seek out food in random direction. There is clearly a southerly departing azimuth. The second is that, contrary to views occasionally expressed in the literature, this species does not depart against the prevailing northeast tradewinds and return with them with full stomachs. The fact that Manana Island brown noddies return against the wind indicates southern feeding grounds may be superior to northeastern areas during summer. Aerial location capability in this study would probably have pinpointed feeding areas.

FUTURE RESEARCH NEEDS

The feeding study needs to be completed and data exhaustively analyzed using automatic data processing. Population estimation techniques need to be refined and access to the NWHI during critical times of the year for censusing purposes needs to be assured.

Physiological work exploring energy metabolism of wild and captive birds with concomitant bomb calorimetry of important prey items should make it possible to model marine resource utilization and energy flow for NWHI seabird populations using techniques similar to Wiens and Scott (1976).



LAAL - Laysan Albatross
BFAL - Black-footed Albatross
BOPE - Bonin Petrel
BUPE - Bulwer's Petrel
WTSH - Wedge-tailed Shearwater
CHSH - Christmas Shearwater
SSPE - Sooty Storm-Petrel
RTTB - Red-tailed Tropicbird
MABO - Masked Booby
RFBO - Red-footed Booby
BRBO - Brown Booby
GRFR - Great Frigatebird
SOTE - Sooty Tern
GBTE - Grey-backed Tern
BRNO - Brown Noddy
BLNO - Black Noddy
FATE - Fairy Tern

Figure 4. Comparative lengths of incubation shifts and chick feeding intervals for 17 Northwestern Hawaiian Islands seabird species (Knudtson and Naughton, in preparation)

Effort needs to be directed towards the location of feeding areas. The radiotelemetry work needs to be expanded and aerial survey transects need to be flown using standard techniques (Harrison and Hall, 1978; Harrison, in press) to locate feeding areas for important NWHI colonies.

To assess the importance and seasonality of important prey items in seabird diets, basic life histories and estimates of annual production

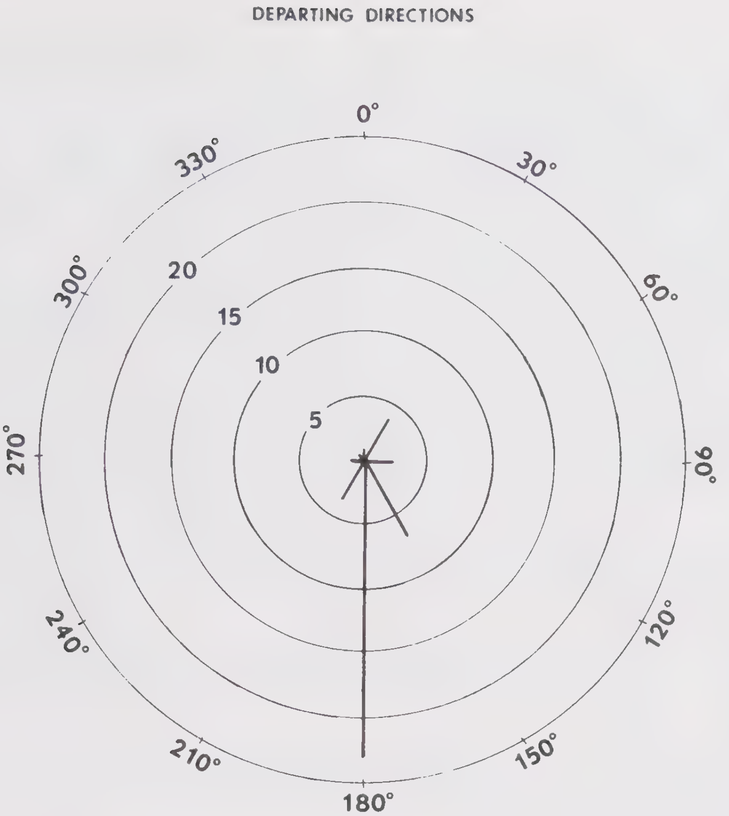

DEPARTING DIRECTIONS

Figure 5. Departing directions of breeding brown noddies from Manana Island. Vector magnitudes signify number of birds detected departing in each 30° sector. (Harrison and Stoneburner, in preparation)

data are needed for Ommastrephidae, Exocoetidae, Mullidae, Synodontidae, and Decapterus sp.

ACKNOWLEDGMENTS

Richard Shomura, Southwest Fisheries Center Honolulu Laboratory, made this work possible in innumerable ways. Mike Seki provided invaluable assistance in the laboratory. Richard Young consented to help identify the squid, a most difficult group. It is a pleasure to thank these people.

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8024

INTRODUCTION

Elizabeth D. Haynes[1] and Douglas R. McLain[2]

This report is the fifth in an evolving annual series intended to provide fishermen and resource managers with a convenient synopsis of the marine environment.[3] The objective of the reports in this series is to describe in a timely manner the gross features of the marine environmental fluctuations in areas of interest to American fishermen, fishery biologists, and managers.

The fact that variations in the environment affect the distribution, abundance, and availability of fish has been recognized and studied for at least eighty years by the Council for the Exploration of the Sea and successor organizations. Such studies are a continuing effort of the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program of the National Marine Fisheries Service (NMFS). MARMAP is a major source of biological and other scientific information needed for management of the nation's fishery resources under P.L. 94-265, the Fishery Conservation and Management Act (FCMA) of 1976.

Duties and activities of MARMAP include the collection and analysis of the biological, chemical, and physical oceanographic data needed to provide basic information on the abundance, location, and condition of the commercial and recreational fishery stocks within the U.S. fishery conservation zone.

A major emphasis of MARMAP in recent years has been to develop mathematical models of marine populations, leading to improved methods for predicting fishery yields. Knowledge of environmental factors, particularly during critical phases of the development of a year class, and of the effects of variations of these factors, has proved to be of great importance in these models.

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[1] Resource Assessment Division, National Marine Fisheries Service, NOAA, Washington, DC 20235.

[2] Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940.

[3] Previous volumes in this series are:

Goulet, J. R., Jr. (compiler). 1976. The environment of the United States living marine resources - 1974. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., MARMAP Contrib. 104, 375 p.

Goulet, J. R., Jr.,and E. D. Haynes (editors). 1978. Ocean variability: Effects on marine fishery resources - 1975. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 416, 350 p.

Goulet, J. R., Jr.,and E. D. Haynes (editors). 1979. Ocean variability in the U.S. fishery conservation zone, 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 427, 362 p.

Pedrick, R. A., M. C. Ingham, D. R. McLain, J. Namias, and others. 1979. Marine environmental conditions off the coasts of the United States, January 1977-March 1978. Mar. Fish. Rev. 41(5-6): 20-69.

All are available on request from NOAA, NMFS, F/SR2, 3300 Whitehaven Street, N.W., Washington, DC 20235.

Historically, each species has been managed as if it existed alone in a stable or "average" environment. Modern computers have made it possible to express interrelationships among species mathematically and thus to develop "ecosystem" models. The various effects of the environment and its variations in time and space on the different species of the ecosystem can also be included in the model. The changing of controllable factors, such as harvest rates and total annual catches, can be tested before the fishing season by "running" the model on the computer under various assumptions to determine which fishing strategies appear to be most productive and least damaging to the stocks.

Scientists within NMFS have considerable expertise in fisheries analysis and population dynamics. The Atlantic and Pacific Environmental Groups within NMFS were created under the MARMAP program to apply environmental data to the solution of fisheries problems. Notable progress has been made in many cases, with considerable success in several instances, by using the modeling approach and including environmental parameters. Annual environmental reports are issued by the Environmental Groups in cooperation with the Fishery Research Centers and others.

This volume presents an overview of the climatological variations of the year 1978 and first quarter of 1979, and mentions possible environmental effects on species of interest to commercial fisheries. It reflects the availability of recent oceanographic information as well as the authors' judgement regarding those parameters which affect marine populations.

Information on fluctuations of ocean circulation would be particularly desirable in these reports, but routine measurements of ocean currents are sparse and not directly intercomparable. It is necessary to use indirect measures of ocean circulation such as calculations of Ekman transport and upwelling indices, and measurements of sea level and sea-surface temperatures (SST) to infer circulation changes. Also, it is desirable to look first at the atmospheric large-scale driving forces of the ocean as an aid in understanding the smaller-scale regional oceanographic and biological effects. Therefore the report first presents descriptions of the large scale fluctuations in atmospheric circulation, surface (Ekman) transport, upwelling, sea level, and SST to define the major changes in oceanic conditions during the period and relative to prior years. Discussions of regional fluctuations of SST, salinity, river discharge, and biological factors are then presented for areas along the Pacific coast of North America from the eastern Bering Sea to the eastern tropical Pacific and along the Atlantic Coast from the Gulf of Maine to the Gulf of Mexico.

The data presented in this report are primarily physical, since such data are available more widely and more rapidly than biological observations. It is hoped that these descriptions will be of use to biologists in identifying unusual observations of marine organisms and relating them to environmental events. The authors encourage readers to note and report unusual biological occurrences. Such reports are published in periodicals such as the University of Rhode Island's quarterly newsletter, Coastal Oceanography and Climatology News, which includes unusual observations from both the Pacific and Atlantic coasts. A form for reporting unusual biological observations in Alaska has been developed by Dr. R. R. Straty of the NMFS laboratory at Auke Bay, AK 99821, and Alaskan readers are encouraged to submit reports to him. Many other sources of data on oceanographic fluctuations are available. Fishing Information is published monthly by the Southwest Fisheries Center, NMFS, La Jolla, CA 92038. It contains maps of monthly mean surface pressure, winds, and SST, and a vertical section of subsurface temperature in the Pacific. The gulfstream, published monthly by the Oceanographic Services Branch, National Weather Service, Silver Spring, MD 20910, focuses on Gulf Stream eddy activity and SST's and their anomalies off the U.S. east coast. The Monthly Weather Review and Weatherwise are published under the sponsorship of the American Meteorological Society, Boston, MA 02108, and provide monthly descriptions of weather conditions. National Fisherman, Camden, ME 04843, is a monthly newspaper with many articles of interest to the oceanographic community as well as to the commercial fisherman, including effects of weather. The reader is referred to these sources for additional details on environmental fluctuations and for timely updates of changing conditions.

In view of the availability of information from the other established sources listed above, this series will be discontinued with this volume. The Atlantic and Pacific Environmental Groups will continue to issue their annual reports and will respond directly to specific requests from NMFS users for oceanographic data and other information.

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THE STRUCTURE OF REEF FISH COMMUNITIES IN THE HAWAIIAN ARCHIPELAGO: INTERIM STATUS REPORT

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ABSTRACT

The structure of reef fish communities in the Hawaiian Archipelago is being studied as part of a broad investigation of marine resources in the Northwestern Hawaiian Islands. To date, communities have been sampled at eight islands or island groups: Kure, Midway, French Frigate Shoals, Necker, Nihoa, Niihau, Oahu, and Hawaii. Other locations will be sampled soon. The following generalizations are evident in the data collected so far, but remain tentative until sampling has been completed. (1) Forces that determine the distribution patterns involve either environmental factors (including biological interactions) or fishing pressures. (2) Northwestern communities show close ties with communities in both the warm temperate and the tropical western Pacific, but southeastern communities show close ties only with communities in the tropical western Pacific. (3) The predominant members of the northwestern communities, as a group, are better attuned to the overall Hawaiian environment than are the predominant members of the southeastern communities. They show this by being more evenly distributed over the archipelago and by including proportionally more endemics. (4) Many species prominent in shallow-water communities in the northwest occur only in deeper water southeastward. (5) The southeastward distributions of species in the northwestern communities are limited by both environmental factors and fishing pressures, but the northwestward distributions of species in the southeastern communities are limited only by environmental factors.

fishes
Hawaii
fish communities
zoogeography

INTRODUCTION

Our knowledge of reef fishes in Hawaii is based almost entirely on what is known of the inhabitants of reefs surrounding the high islands. We know little of the fishes that live on reefs around those low bits of land and expansive shallows that stretch more than 1,500 km northwestward from the high island of Kauai. These are the Northwestern Hawaiian Islands, a vast region that constitutes less than 1% of the land area in the archipelago, but about 65% of the marine environment between shore and 100 fathoms (Bryan, 1954). Clearly the reef resources here, still virtually untouched by humans, greatly exceed those of the long exploited high islands.

Not only do the reefs of the Northwestern Hawaiian Islands encompass greater area, they also include more varied habitats. Although each of the high islands offers many distinct reefs, it is a mix that tends to be repeated from island to island. Probably this is because each high island presents a similar underwater setting. Being in essence one or more large volcanic peaks that block the prevailing wind and seas, they support distinctive windward and leeward reefs. And the area available for shallow reefs around these islands tends to be limited to relatively narrow shelves, beyond which the seafloor drops sharply to great depths.

In comparison, shallow reefs exist in highly dissimilar circumstances from one end of the Northwestern Hawaiian Islands to the other. In part, this is because they cover almost three times the distance and more than twice the latitude covered by the high islands. Probably more important, however, their topographies are more varied. Nihoa and Necker are most like the high islands, being small volcanic peaks that rise abruptly from the sea. But they offer no appreciable lee, and both rest on broad submerged platforms that provide more suitable depths for shallow habitats than do the comparatively narrow shelves that surround the high islands. Northwestward from Necker, conditions progressively become even more different. At French Frigate Shoals exposed volcanic rock is limited to La Perouse Pinnacle, an anomalous basaltic structure that juts from amid expansive shallows and low sandy islets. This and Gardner Pinnacles--two precipitous volcanic rocks surrounded by a broad submerged platform--are the last bits of exposed basalt to the northwest. Farther on, Maro Reef is the almost totally submerged crest of an oval-shaped seamount, whereas Laysan and Lisianski are low sandy islands surrounded by wide shallows. Finally, Pearl and Hermes, Midway, and Kure are coral atolls, even though they lie at high latitudes.

This great diversity of reef habitats strongly influences how fishes are distributed over the archipelago. Because a species is defined by a combination of characteristics adapted to specific environmental conditions, it should be most successful where those conditions are best approximated. Thus, its distribution should reflect its environmental requirements. The importance of this concept to those that would manage Hawaiian fishes is obvious. If we know both the requirements of a species and the characteristics of a habitat, we should be able to predict that species occurrence in that habitat. And where the occurrence fails to meet the prediction, it should be possible to identify the root of the discrepancy.

So, I believe that study of how Hawaiian reef fishes are distributed over the archipelago will identify many of the forces that shape their communities.

Several other investigations, past and present, contribute to this effort. The project is based on my earlier study of reef fishes at Kona, Hawaii (Hobson, 1972, 1974) and is closely tied to current studies of the reef benthos (see paper by Grigg and Dollar) on the same reefs. And because I believe that trophic relationships are the major forces shaping the structure of reef fish communities, I expect valuable interaction with the current studies of trophic relationships among fishes in the Northwestern Hawaiian Islands (see paper by Parrish et al.).

This is a preliminary report on the project's current status. Anticipated contributions to the scientific literature include the distribution patterns of certain key species done in collaboration with Leighton Taylor, and an analysis of ecological relations in distribution patterns done in collaboration with Richard Grigg.

METHODS

This study is based on direct observations, using SCUBA, of reef communities between shore and depths of 20 to 35 m. Work at each island begins with a general reconnaissance where representative habitats are identified and all species seen are listed. Having acquired a general familiarity with the area and its fauna, 25 x 4 m transect lines are established in the representative habitats. My experience with transect counts to assess fish communities under varied conditions has shown this to be an effective sample area. A longer line too often cannot be contained within a single type of habitat. Cryptic forms escape notice when more than about 2 m from the line. Also, the standard 72 cu. in. diving tank provides just a bit more air than it takes to complete a count at the deeper stations.

The counts are made as follows. The preliminary reconnaissance and previous experience have established species likely to be present, their relative numbers, and their general behavior. As I lay out the line (a fiberglass metric measuring tape), moving rapidly, I count those species that tend to avoid humans. Then I return along the line, counting those species that are attracted to humans, but moving fast enough to avoid repeated counts of those individuals that follow. Finally, I move slowly back along the line, carefully inspecting crevices for cryptic, sedentary forms that readily go unnoticed. I spend 40 min. on each count so that each habitat receives equal attention, and during this time note any fish within the sampled area that I have reason to believe was not counted earlier. The tally generally includes more individuals than are in the area at one time. With the limited number of counts I am able to make, this methodology has proven the most effective way to determine which species frequent the sampled habitat. It does not, however, provide data for projections of biomass.

To make the counts more accurately reflect community structure, it is necessary to make an adjustment for certain species, generally grazing acanthurids or scarids, that roam over the reef in exceptionally large aggregations. Typically these aggregations include several hundred individuals, and experience has shown that their chance entry--or non-entry--into the sample area will produce a distorted picture of community structure. The problem is exaggerated in this study because there is opportunity for just a relatively few transect counts in any one place. I have concluded that it is best to record these schools (estimates of the number of individuals) as footnotes, whether or not they enter the same area, and not use them in calculating the index used to characterize community structure. This procedure seems to be working out. Generally when such schools are present there are enough conspecifics present apart from these large schools to rank the species among the major components of the community.

The counts are not without inherent bias. Generally, highly cryptic forms like muraenid eels are grossly underrepresented. In some habitats the same is true of certain nocturnal species, like holocentrids, that spend the daytime under cover. And although the water was clear enough at all stations to include the entire water column in the counts, certain very small species like atherinids and engraulids that school just under the surface were not included because their numbers, and sometimes their identities, could not be determined consistently in observations made from the seafloor. These problems, however, applied equally to all counts, so do not weaken the comparisons.

Finally, I did not count small juveniles because their numbers vary greatly with the season and from year to year for reasons unrelated to conditions on the reef. Their inclusion would, in fact, obscure, rather than clarify, the adaptiveness of the established adult to the habitat under study.

Following the transect count, I inspect the surrounding area for other species, noting their relative abundance, and any indications that the transect counts might have produced a misleading assessment of the community. These supplemental observations contribute to the interpretations drawn from the transect data and are especially important as added support when a species is noted to be absent.

Eight islands, or groups of islands, have been sampled to date (Table 1).

RESULTS

Temporal variations in community structure

The communities at different locations in the archipelago are being sampled at different times--often one or more years apart. There would be serious problems with the comparisons if the communities change much from year to year. But their major components, at least, remain essentially unchanged over the period of time involved here, as determined by transect counts made at Kona over three years and at Midway over two years. Because space is limited here, I present data from just one site at each location (Tables 2 and 3), but two other sites at Kona and

TABLE 1. STATIONS WHERE THE FISH COMMUNITIES HAVE BEEN SAMPLED WITH TRANSECT COUNTS AND OTHER OBSERVATIONS, JULY 1977 TO SEPTEMBER 1979

Island	Dates	No. Transect Sites	No. Transects	Depth (m)	Depths of General Obs. (m)
Hawaii	7/77; 10/78; 9/79	3	36	2-12	shore to 35
Oahu	7/77; 11/77; 10/78; 5/79; 9/79	2	8	7-10	shore to 35
Niihau	11/78	2	4	7-10	shore to 20
Nihoa	11/78	2	4	8-10	shore to 35
Necker	11/78	1	2	15	shore to 20
Fr. Frig. Sh.	11/78	5	8	9-12	shore to 20
Midway	8/77; 9/79	8	16	2-12	shore to 35
Kure	8/77; 9/79	8	14	2-12	shore to 35

TABLE 2. MAJOR SPECIES ON ONE CORAL REEF AT KONA, HAWAII

1977 Rank	Species	Relative Abundance Index[1]		
		1977	1978	1979
1	*Chromis agilis*	19.1	18.0 (1)[2]	18.5 (1)
2	*Ctenochaetus strigosus*	12.7	15.8 (3)	15.4 (2)
3	*Zebrasoma flavescens*	12.1	16.6 (2)	13.8 (3)
4	*Chaetodon multicinctus*	8.4	10.1 (4)	8.3 (4)
5	*Chromis vanderbilti*	6.3	0.9	4.7 (5)
6	*Thalassoma duperreyi*	6.1	4.4 (5)	3.4 (7)
7	*Acanthurus nigrofuscus*	4.4	1.7 (9)	1.0
8	*Plectroglyphidodon johnstonianus*	3.3	3.0 (7)	1.8 (8)
9	*Centropyge potteri*	3.1	3.3 (6)	3.8 (6)
10	*Chromis hanui*	2.4	2.8 (8)	1.8 (8)
		4 transects $\bar{x}$ no. sp. 34 $\bar{x}$ no. ind. 185	4 transects $\bar{x}$ no. sp. 33 $\bar{x}$ no. ind. 159	4 transects $\bar{x}$ no. sp. 35 $\bar{x}$ no. ind. 191

[1] Relative Abundance Index is the percent of all individuals counted that were of this species.

[2] Numbers in parentheses indicate rank that year if in top 10.

TABLE 3. MAJOR SPECIES OUTSIDE WINDWARD REEF AT MIDWAY ATOLL (ONE LOCATION)

1977 Rank	Species	Relative Abundance Index[1] 1977	Relative Abundance Index[1] 1979
1	*Acanthurus triostegus*	16.3	11.7 (3)[2]
2	*Chromis ovalis*	14.2	13.9 (1)
3	*Acanthurus leucopareius*	12.3	12.8 (2)
4	*Myripristis amaenus*	7.0	6.1 (7)
5	*Stegastes fasciolatus*	6.3	8.5 (5)
6	*Kyphosus cinerascens*	5.4	4.9 (8)
7	*Thalassoma duperreyi*	4.9	8.5 (4)
8	*Acanthurus nigroris*	4.7	0.4
9	*Abudefduf abdominalis*	2.7	7.6 (6)
10	*Thalassoma ballieui*	1.9	2.9 (9)
		2 transects $\bar{x}$ no. sp. 33 $\bar{x}$ no. ind. 316	2 transects $\bar{x}$ no. sp. 35 $\bar{x}$ no. ind. 223

[1] Relative Abundance Index is the percent of all individuals counted that were of this species.

[2] Numbers in parentheses indicate rank that year if in top 10

another at Midway produced similar results. Not only do the same species predominate from year to year, but they do so in approximately the same relative numbers. It is important that this condition exists at both ends of the archipelago, because fish community structure can be more changeable at higher latitudes (unpublished data).

Spatial variations in community structure

I have yet to sample certain important locations in the archipelago, e.g., Gardner Pinnacles, Maro Reef, Laysan, and Pearl and Hermes, so many relationships remain unexamined. Nevertheless, data now in hand illustrate certain patterns that probably are significant.

Because the reef habitats change progressively from one end of the archipelago to the other, it is meaningful to compare conditions on the island of Hawaii with those at Midway-Kure. It is striking that the major species at Kona tend to lose dominance northwestward until they are rare or absent at Midway-Kure (Table 4), whereas the major species at Midway-Kure, while they tend to decline somewhat in relative numbers southeastward, nevertheless are generally more evenly distributed over the archipelago (Table 5).

TABLE 4. NORTHWESTWARD OCCURRENCES OF MAJOR SPECIES[1] ON TRANSECT LINES AT KONA, ISLAND OF HAWAII

Species	Hawaii	Oahu	Nihoa	French Frigate S.	Midway-Kure
Chaetodon multicinctus	****	**	**	**	●
Plectroglyphidodon imparipennis	****	●	**	*	0
Chromis agilis	****	●	0	*	0
C. vanderbilti	****	****	****	****	●
Acanthurus nigrofuscus	****	****	****	****	0
Zebrasoma flavescens	****	***	●	*	●
Ctenochaetus strigosus	****	****	**	****	**

[1] Listed are the species that represented >10% of all individuals counted on any one of the 36 Kona transect lines. Asterisks represent the largest percent of all individuals counted that were of that species on any one transect line at each location.

**** = >10%   *** = 5-9%   ** = 1-4%   * = <1%
● = seen (but not on transect)   0 = not seen

TABLE 5. SOUTHEASTWARD OCCURRENCES OF MAJOR SPECIES[1] ON TRANSECT LINES AT KURE AND MIDWAY ATOLLS

Species	Kure-Midway	French Frigate S.	Nihoa	Oahu	Hawaii
Myripristis kuntee	****	●	●	*	**
Flammeo sammara	****	●	●	●	*
Kyphosus cinerascens	****	**	****	●	**
Mulloidichthys flavolineatus	****	●	●	●	**
Chromis ovalis	****	****	****	●	●
Dascyllus albisella	****	***	●	●	●
Stegastes fasciolatus	****	**	**	***	***
Thalassoma duperreyi	****	***	***	***	***
T. ballieui	****	**	**	**	*
Scarus dubius	****	**	●	0	*
S. sordidus	****	**	●	●	*
Acanthurus leucopareius	****	**	**	●	***
A. nigroris	****	**	**	**	***
A. triostegus	****	**	**	**	***

[1] Listed are the species that represented >10% of all individuals counted on any one of the 30 Midway to Kure transect lines. See footnote 1 of Table 4 for explanation of symbols.

I believe that the combination of exploratory reconnaissances, general observations, and transect counts produced reasonable species lists for most locations. If so, the patterns of occurrence of even the relatively minor species in these lists can be meaningful. The data show that 21 of the species seen more than once on transect lines at Kona were not seen on transects or during other observations at Kure or Midway, and 12 of the species that recurred on the transect lines at Kure and Midway were not seen on transects or during other observations at Kona (Table 6).

Generally the comparisons drawn in this report are limited to observations made during this study. This is to reduce the bias that would otherwise stem from my many observations in the high islands, especially Hawaii and Oahu, during previous years. It is significant, however, that during all of my intensive work at Kona, I saw only one of the species listed in part II of Table 6--an occasional *Caranx ignobilis*. Similarly, two other species--the histiopterid *Histiopterus typus* and the pomacanthid *Genicanthus personatus*--seen repeatedly on reefs as shallow as 20 m at Midway and Kure (though not on transect lines) have not been seen in the high islands.

The shift in community structures from one end of the archipelago to the other is not a smooth progression. The various islands, and certain groups of islands, have distinct features that influence their fish communities. This was most evident at French Frigate Shoals. Two relatively common species, *Chaetodon trifascialis* and *Chaetodon citrinellus*, were not seen elsewhere in the archipelago during this study. *Chaetodon trifascialis* invariably occurred with coral of the genus *Acropora*, which dominated some reefs there, but is rare or absent elsewhere in the archipelago (see paper by Grigg and Dollar). An additional feature of fish communities in the Northwestern Hawaiian Islands is the relatively high incidence in shallow water of the large terminal male phase of many labrid species. Most prominent are: *Bodianus bilunulatus*, *Coris flavovittata*, *Anampses cuvier*, *Thalassoma purpureum*, and *Thalassoma ballieui*. These are especially numerous at Midway and Kure.

DISCUSSION

It is premature to draw broad generalizations about the structure of reef fish communities throughout the archipelago because too many critical locations remain unsampled. Nevertheless, the data in hand suggest certain patterns likely to be strengthened by future sampling.

Because conditions differ so from one end of the archipelago to the other, it is not surprising that dominant species vary from place to place. Forces likely to limit distribution of the various species fall broadly in one of two categories: environmental factors (including biological interactions) and fishing pressures.

Undoubtedly, a great variety of environmental pressures exist in the wide range of reef habitats between the island of Hawaii and Kure Atoll. These would be expected to influence both the northwestward distribution of species more prominent in the southeast (such as those at Kona, Tables 4 and 6, part I), and the southeastward distribution of species more

TABLE 6. SPECIES THAT RECURRED ON TRANSECT LINES AT ONE END OF THE ARCHIPELAGO, BUT WERE NOT SEEN AT ANY TIME AT THE OTHER END

I.	Species that recurred at Kona[1]	Most northwestward sighting
1.	*Cephalopholis argus*	Niihau
2.	*Aphareus furcatus*	French Frigate Shoals
3.	*Monotaxis grandoculis*	" " "
4.	*Parupeneus bifasciatus*	Niihau
5.	*Chaetodon ephippium*	Nihoa
6.	*C. reticulatus*	Kona
7.	*C. lineolatus*	"
8.	*Plectroglyphidodon sindonis*	French Frigate Shoals
9.	*Coris gaimard*	" " "
10.	*Thalassoma fuscus*	" " "
11.	*T. quinquevittata*	" " "
12.	*Scarus rubroviolaceus*	" " "
13.	*Ctenochaetus hawaiiensis*	" " "[2]
14.	*Naso lituratus*	" " "
15.	*N. brevirostris*	" " "
16.	*Plagiotremus goslinei*	Necker
17.	*Rhinecanthus rectangulus*	"
18.	*Cantherines sandwichiensis*	French Frigate Shoals
19.	*Pervagor melanocephalus*	Kona
20.	*Ostracion solorensis*	"
21.	*Canthigaster amboinensis*	French Frigate Shoals

II.	Species that recurred at Midway-Kure	Most southeastward sighting
1.	*Carcharhinus amblyrhynchos*	Nihoa
2.	*Ostichthys pilwaxii*	Midway
3.	*Epinephelus quernus*	"
4.	*Oplegnathus fasciatus*	"
5.	*O. punctatus*	"
6.	*Goniistius vittatus*	French Frigate Shoals
7.	*Caranx ignobilis*	Necker
8.	*C. cheilio*	Midway
9.	*Carangoides ferdau*	"
10.	*Epibulus insidiator*	French Frigate Shoals
11.	*Cheilinus bimaculatus*	Oahu
12.	*Cheilio inermis*	"

[1] Other than species listed in Table 4.

[2] William Walsh, University of Hawaii, personal communication, November 1978.

prominent in the northwest (such as those at Kure-Midway, Tables 5 and 6, part II). Fishing pressure, too, would be expected to have an impact. But because, historically, fishing by humans has been concentrated in the southeastern part of the archipelago, a measurably impact would be expected only in the southeastward distributions of certain species more prominent in the northwest.

Environmental factors that limit distribution northwestward

All of the species more prominent at Kona (Tables 4 and 6, part I) demonstrate a close relationship with fishes in more southerly waters of the tropical western Pacific. Even the one Hawaiian endemic among the major forms--*Chaetodon multicinctus*--has a close Indo-West-Pacific analog, *C. punctatofasciatus* (Gosline, 1956). From this evidence alone one might expect these species to be limited northward by lower water temperatures, and undoubtedly many are. But at least over the southeastern half of the archipelago--from the island of Hawaii to French Frigate Shoals--it seems that other environmental factors are more powerful than water temperature in determining the distribution patterns of at least some species.

Consider, for example, *Acanthurus nigrofuscus*, which Randall (1960, p. 248) reported to be "...probably second in abundance among surgeonfishes in Hawaii only to the manini" (*A. triostegus*). Based on its occurrences in a variety of habitats during this study, *A. nigrofuscus* is dominant only where much of the seafloor is exposed basalt--a widespread feature of high-island reefs. Its dependence on some factor related to exposed basalt seems evident through the Northwestern Hawaiian Islands as far as French Frigate Shoals, where its prominence is confined to La Perouse Pinnacle, the only location there with exposed basalt. *A. nigrofuscus* was not seen at Midway or Kure, where exposed basalt is absent.[1] A similar dependence on some factor associated with exposed basalt, but with an added feature associated with surge-swept shallows, is suggested in the distribution patterns of the pomacentrids *Plectroglyphidodon imparipennis* and *P. sindonis*.

It would also appear that forces other than those associated with water temperatures limit the distribution of *Zebrasoma flavescens* into the Northwestern Hawaiian Islands. In this case, the limiting factor seems related to the absence there of well-developed lee shores. On the high islands--at least Oahu and Hawaii--this species is prominent only in certain leeward habitats (Brock, 1954).

Despite the low water temperature during the winter at French Frigate Shoals, the reef habitats are more favorable to at least some Indo-West-Pacific forms than are reef habitats in the high islands, such as corals of the genus *Acropora* and the co-occurring butterflyfish *Chaetodon trifascialis*. These species, common throughout most of the tropical Indo-Pacific region, are rare or absent from most of the Hawaiian Archipelago, in the south as well as in the north.

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[1] The apparent relation of *Acanthurus nigrofuscus* to exposed basalt in Hawaii is questioned by the widespread prominence of *A. elongatus*--considered synonymous with *A. nigrofuscus* by Randall (1956)--on basaltless coral reefs of the Marshall Islands (Schultz and Woods, 1953).

The butterflyfish Chaetodon citrinellus is another species widespread in the Indo-Pacific region and common at French Frigate Shoals, but was unseen elsewhere during this study. Gosline and Brock (1960) considered it to be rare in Hawaii.

The element favorable to certain Indo-West-Pacific species in reef habitats at French Frigate Shoals, but not around the high islands, is unknown. Perhaps barrier reefs that enclose expansive shallows--a prominent setting here and in the western Pacific, but limited around the high islands--establish some required element. Barrier reefs are widespread northwestward from French Frigate Shoals to Midway and Kure. I am anxious to sample the intervening islands--Gardner Pinnacles, Maro Reef, Laysan, Lisianski, and Pearl and Hermes--to determine where the various Indo-West-Pacific forms prominent at French Frigate Shoals, but absent at Midway-Kure, drop out. Because Midway and Kure are coral atolls, they must satisfy many of the environmental requirements of these species. But water temperatures on shallow reefs there drop below 18°C (Mauck, 1975), which probably are intolerably for many. However, low water temperatures have not limited Epibulus insidiator. This Indo-West-Pacific labrid apparently finds some needed environmental feature on reefs from French Frigate Shoals to Kure Atoll that is lacking on the volcanic islands to the southeast.

Environmental factors that limit distribution southeastward

The major species at Midway-Kure (Table 5), like the major species at Kona, discussed above, are closely related to fishes on the tropical western Pacific. But considered together, they probably are more representative of the Hawaiian fauna than is the Kona group. More evenly distributed over the archipelago, the Midway-Kure group includes four Hawaiian endemics (Chromis ovalis, Dascyllus albisella, Thalassoma duperreyi, and T. ballieui), compared to only one (Chaetodon multicinctus) in the other groups. Hence, the Midway-Kure group would seem generally more attuned to the Hawaiian environment.

A new element enters the discussion, however, when we consider those species less numerous than the above which nevertheless occurred in Midway-Kure transect counts, but absent at Kona (Table 6, part II). Among these are species that demonstrate close ties with more temperate regions of the western Pacific. Both Oplegnathus fasciatus and O. punctatus are prominent in coastal waters of Japan, where they are popular game fishes (Masuda et al., 1975). Despite their common occurrences at Kure and Midway they are rare southeastward in the Hawaiian chain. Oplegnathus punctatus has not been recorded in Hawaii until now and O. fasciatus has been recognized from just one specimen taken almost a century ago. Gosline and Brock (1960) considered it a dubious record.

Similar ties to warm temperate western Pacific habitats are suggested by the frequent occurrences on shallow (10 to 20 m) reefs of Ostichthys pilwaxii and Goniistius vittatus, as well as Histiopterus typus (which were not counted on transect lines but were seen repeatedly elsewhere). Both O. pilwaxii and H. typus occur in Japanese waters, as do close relatives of G. vittatus (Masuda et al., 1975), but here still another dimension enters the discussion: variations in depth of occurrence with latitude. Although H. typus appears to be genuinely rare to the southeast [Gosline and Brock (1960) were aware of just two specimens], the populations of O. pilwaxii and G. vittatus seem limited to deeper water. Based on experience centered in the high islands, Gosline and Brock (1960) made no mention of O. pilwaxii (as O. japonicus) being uncommon, but noted (p. 143) that it "...is probably the deepest water species of all the holocentrids." And they reported (p. 203) that G. vittatus (as Cheilodactylus vittata) is "...not uncommon in water about 100 feet deep."

It is a well recognized principle of zoogeography that fishes widely distributed over latitude occur in deeper water toward the equator (e.g., Hubbs, 1948). Furthermore, studies along the North American west coast, where the pattern is reversed with local upwelling, have shown that the phenomenon is based on water temperatures (Hubbs, 1948). So we should expect a straightforward relation between depth and water temperature to account for the distributions of at least some of the species that inhabit shallow reefs in the northwest, but only deeper reefs further south. This may account for the distribution of the angelfish Genicanthus personatus, for example, which is relatively common on reefs 20 to 30 m deep at Midway and Kure, but which has been reported only from deep water around the high islands (Randall, 1975). And it may explain why the large terminal male phase of the labrid Bodianus bilunulatus lives on reefs as shallow as 1 to 2 m at Midway and Kure, but at Kona rarely occurs in shallower depths than 20 m. It may even account for the similar distribution of the grouper Epinephelus quernus, which I found to be numerous in water as shallow as 5 m at Kure and Midway, but which frequents fairly deep water southeastward (Gosline and Brock, 1960). In this last case, however, the situation is clouded by yet another consideration--fishing pressures.

The impact of fishing pressures on distribution

The absence of fishes like Epinephelus quernus in shallow water to the southeast might reflect increased fishing pressures. Certainly E. quernus is an easy mark for spear fishermen, who without doubt have taken a heavy toll of shallow-water reef fishes around the high islands. Similar uncertainty surrounds the southeastward occurrences of Caranx cheilio. This species was represented on transect lines at Midway that were in depths of 5 m (Table 6, part II), but it was not seen at French Frigate Shoals or southward. Does this reflect fishing pressures or restriction to deeper water in the south?

The marked decrease in numbers of some species southeastward cannot be attributed to population shifts into deeper water, however, because they inhabit shallow reefs throughout the archipelago. Certainly the distribution patterns of some, like the shark Carcharhinus amblyrhynchos, may find some environmental feature of high-island reefs unfavorable, as they seem generally sparse there. Others, however, are known to thrive on reefs of the high islands, and their current low numbers in the study areas likely reflect fishing pressures. Considering just those listed in

Tables 5 and 6, part II, we can point to *Myripristis kuntee* and *Caranx ignobilis*. *Myripristis kuntee* is well known to be a prime target of spear fishermen, and *C. ignobilis* is coveted by spear fishermen and shore fishermen alike. A similar appraisal of the species more prominent in the south (Tables 4 and 6, part I) fails to suggest species likely to be subjected to strong fishing pressures. Of the species listed, only the grouper *Cephalopholis argus* and the snapper *Aphareus furcatus* would seem likely possibilities. *Cephalopholis argus*, however, has in fact been expanding its range northward since it was introduced into the high islands from Tahiti several decades ago, and *A. furcatus*, a relatively small, generally solitary species, is not particularly sought after.

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AGE DETERMINATION AND AGE RELATED FACTORS IN THE TEETH OF WESTERN NORTH ATLANTIC BOTTLENOSE DOLPHINS

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ABSTRACT

Teeth were taken from 120 bottlenose dolphins, *Tursiops truncatus*, which had stranded on the mid-Atlantic coast of the United States. The number of annual growth layer groups (GLGs) for each animal was used to construct a growth curve. The growth rate of coastal North Atlantic Ocean *Tursiops* is similar to other cetaceans in having a high initial rate of growth, with no differences in growth between females and males. In females, the first dentinal GLG is thickest and is followed by GLGs which become progressively narrower. In males, the second GLG is thicker than the first; GLGs beyond number two become progressively smaller but at a slower rate than in females. In males and females, the translucent layer makes up proportionally larger parts of the GLG as the animal ages, but in males the percent translucent layer remains constant at about 50% while in females it continues to increase up to about 70% of the GLG. These two factors, GLGs width and translucent layer width, indicate that the sex and age of the animal influence the deposition of GLGs. Incremental layers are also present, averaging 12 per GLG, and seem similar to incremental layers described in other marine mammals. A plot of the relationship of percent growth of the last GLG to time of death suggests that the deposition of GLGs is relatively constant, at least during the first half of the year, and that North Atlantic Ocean *Tursiops* give birth in the fall as well as in the spring.

INTRODUCTION

Owen (1845) documented the existence of "concentric layers of dentine" in odontocete teeth and, similarly, the "appearance of opaque striae or conecntric layers" (pg. 512) in polished sections of pinniped teeth. Lankester (1867) also noted a layering pattern in the teeth of a beaked whale, *Ziphius sowerbiensis* (=*Mesoplodon bidens*), but did not suggest a reason or use for them. In 1950, Scheffer suggested using these layers as a method of age determination when he found layers in the dentine and cement of a fur seal, *Callorhinus ursinus*, canines that corresponded to the known age of seals branded as pups and recovered up to eight years later. Laws (1952, 1953) suggested using dentinal layers in odontocete teeth as a measure of age when he found layers in sperm whale teeth similar to those in pinniped teeth. In the following years, dentinal growth layers (growth layer groups) were discovered and used as age indicators in *Stenella coeruleoalba* (Nishiwaki and Yagi, 1953,

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1954), *Berardius bairdii* (Omura *et al.*, 1955), and sperm whales (Nishiwaki *et al*, 1958).

In 1959, Sergeant described growth layer groups (GLGs) in the teeth of four bottlenose dolphins, *Tursiops truncatus*, from Marine Studios in Florida. Two of the animals were born and died in captivity; two were wild caught and died in captivity. In each case the number of GLGs in the teeth corresponded with the known or estimated age of the animals based on their time spent in captivity. The oldest animal was estimated to be 15.5 years old and had 17 GLGs. He also examined a few teeth from the pilot whale, *Globicephala melaena*, and one each from the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, and the common dolphin, *Delphinus delphis*. All of the species demonstrated layering in the dentine similar to that of *Tursiops*, which was identical to that described by Nishiwaki and Yagi (1953) for *S. coeruleoalba*.

Since Sergeant's paper, dentinal GLGs have been used extensively for age determination of odontocetes. Most of the work has centered on direct application of the technique, predominantly for species involved in fisheries, for example, sperm whale (Gambell and Grzeborzewska, 1967; Best, 1970; Gambell, 1977), delphinids (Sergeant, 1962, 1973; Kasuya, 1972, 1974, 1976; Sergeant *et al.*, 1973; Kasuya *et al.*, 1974; Perrin *et al.*, 1976, 1977; Ross, 1977), the white whale (Sergeant, 1962), Baird's beaked whale (Kasuya, 1977), harbor porpoise (Nielsen, 1973; Gaskin and Blair, 1977) and Dall's porpoise (Kasuya, 1978). However, some aspects of age determination and age related factors visible in the teeth of odontocetes have been examined but not satisfactorily explained in many species. Some of these include description and clear identification of GLGs, formation rate of the layers, identification of accessory layers and the more recently discovered incremental layers, and sexual dimorphism.

Since GLGs were first suggested as a means of aging odontocetes much controversy has prevailed over the meaning of these layers, but for the most part the assumption has been that GLGs are deposited annually. However, in a few species evidence based on relative age indices indicates that GLGs are not annual. In the white whale, *Delphinapterus leucas*, Sergeant (1962) and Brodie (1969) have shown circumstantially that more than one GLG is deposited at least during the early growth of the animal, although Khuzin (1961) felt that only one GLG is formed each year. In the narwhal, *Monodon monoceros*, a species related to the white whale, Hay (in press) also feels that more than one GLG is formed. Kleinenberg and Klevezal (1962) found twice as many dentinal GLGs as maxillary bone layers in the Black Sea dolphin, *Delphinus delphis*. In sperm whales, Ohsumi *et al.* (1963) determined that one GLG is formed each year based on 11 whales captured seven to 16 years after being tagged, a rate which Best (1970) confirmed when he followed the growth of the tooth from samples which extended over six months of the year. Berzin (1961, 1964) and Gambell and Grzegorzwerska (1967), however, concluded from samples taken throughout the year that two GLGs are deposited annually. Perrin *et al.* (1977) suggest three possible hypotheses of rate of deposition of GLGs in the spinner dolphin, *Stenella longirostris*, after examining 2500 specimens, none of which is that just one layer is set down per year. They accepted the hypothesis that 1.5 GLGs are deposited in the first year, while one GLG is deposited in all other years, rather than a rate of 1.5 GLGs per year or 1.5 GLGs per year until puberty and one GLG per year thereafter.

Direct evidence on the rate of dentinal growth has supported an annual formation rate. Sergeant's (1959) finding that the number of GLGs in *Tursiops* teeth correlated with the known age or minimum known age for each animal offered the first measure. Similarly, in 1973, Sergeant *et al.* reported that in three captive *Tursiops* from Marineland of Florida the number of GLGs was approximately equal to the known age of the animal. Klevezal and Kleinenberg (1967) examined captive and wild specimens from nine orders of mammals, including cetaceans, and concluded that GLGs are an annual event. Tetracycline injected specimens have also supported an annual deposition rate of GLGs (Best, 1970; Gurevich and Stewart, in press; Perrin and Myrick, in press).

Divergencies of opinion on the periodicity of GLG formation within a species probably can be attributed to the presence of accessory layers, thin layers similar to the hypomineralized layer of the GLG. Klevezal and Kleinenberg (1967) proposed that all odontocetes form one GLG per year but in some species accessory layers are especially distinct, being almost indistinguishable from an annular layer, so that it appears as though two GLGs are deposited annually in some species. More commonly, however, accessory layers are not quite so distinct and may influence the count of GLGs to the extent that repeated counts on the same tooth by one person or several people tend to give different results (Kasuya *et al.*, 1974; Perrin, 1975; Kasuya, 1977; Kimura, in press; Perrin and Myrick, in press). The clear distinction between an accessory layer and a GLG boundary layer is still not defined in some species, for example, the killer whale (*Orcinus orca*), nor is the cause of accessory layers known.

Before the discovery of "annual" growth layers in dentine, research in dental histology had shown the existence of smaller incremental growth patterns. In 1934, Schour and Smith showed that in the continuously growing rat incisor 16 micrometers of dentine are laid down in 24 hours. In 1935, Schour and Steadman described an incremental stratification, also in the rat incisors, which appear as a succession of dark (well calcified) and light (less calcified) layers, the width of each pair totaling 16 μm. Further examination (Schour and Hoffman, 1939) showed the same 16 μm incremental mineralization pattern in 17 other species including fish, a shark, crocodile, mastodon, and several species of mammals, including man. These lines were later interpreted as incremental lines of von Ebner. Yilmaz, Newman and Poole (1977) described daily von Ebner lines in pig dentine where each band consisted of parallel light and dark portions in thin sections of teeth. These were probably equivalent to 5 μm daily von Ebner lines described by Krauss and Jordan (1965) and Newman and Poole (1974). Von Ebner lines have recently been described from the teeth of *Stenella*, where about 365 lines were counted within GLGs (Myrick, in press). Although their deposition rate has not been measured directly, the frequency of these von Ebner lines in the dolphin teeth suggests that they represent a daily growth pattern.

In 1970, Scheffer found still a different frequency incremental layer in thin sections of a *Dugong* tusk. He described a pattern consisting of "coarse layers" and "fine layers". Kasuya and Nishiwaki (1978) found the same pattern in captive dugongs where they defined coarse layers as annual growth layers or GLGs. There were 10 to 15 fine layers within each coarse layer, so the fine layers were suspected to be deposited on a monthly or lunar cycle. Kasuya (1977) found the "long cycles" (GLGs) in Baird's beaked whale teeth to contain many (11.0 to 13.4) "short cycles". Myrick (in press) noted incremental layers of the same periodicity in thin sections from teeth of several species of dolphins. In addition, scanning electron micrographs of a small sample of etched *Tursiops* teeth also showed subannual incremental layers, larger than von Ebner lines, which probably represent the same growth pattern seen by Myrick and Kasuya, appearing as a finer mineralization pattern within the mineralization pattern of the GLG (Hohn, in press). Although the deposition rate of these incremental layers has not been measured directly, this circumstantial evidence suggests a "monthly" growth or mineralization cycle which may be useful for more precise age determination, possibly back-dating the month of birth in young animals, or a better understanding of the mineralization patterns in dentine.

Sexual dimorphisms have also been described in the teeth of some odontocetes. The identification of sexual dimorphism in the growth of teeth has two advantages. First, skeletal material currently in museum collections that is missing data on sex may be more useful for systematic or other research if the sex can be determined from the material on hand, such as the teeth. Secondly, differences in the growth of teeth or other mineralized tissue probably reflects differences in habits or intrinsic factors between the sexes. These differences may help explain the cause of formation of growth layers.

Van Utrecht (1969) found a sexual dimorphism in the extent that the neonatal line overlaps the cementum in teeth of the harbor porpoise, *Phocoena phocoena*, and a small sample of the white-beaked dolphin, *Lagenorhynchus albirostris*. Although Nielsen (1972) confirmed this finding in the harbor porpoise, it has not been described in other odontocetes. Another sexual dimorphism in the teeth of *Phocoena* is found in the ratio of the width of the opaque layer to the width of the translucent layer (Gaskin and Blair, 1977). In males, this ratio remains constant while in females it decreases steadily with age. Gaskin and Blair (1977) also found differences in the amount of dentine deposited annually, which they attributed to size differences of the sexes at any given age. Similar or additional sexual dimorphisms in the teeth have not been described in other odontocetes.

The purpose of this study is to describe dentinal GLGs and accessory layers, including their appearance and position, in western North Atlantic Ocean bottlenose dolphins; to examine age-related changes in GLG deposition and any sexual dimorphisms in dentinal characteristics; and to construct a growth curve for coastal North Atlantic Ocean bottlenose dolphins.

MATERIALS AND METHODS

The Sample

Teeth were collected by the Smithsonian Institution's Marine Mammal Salvage Program (MMSP) from *Tursiops* stranded along the Atlantic coast of the United States between South Carolina and New Jersey. 118 of these animals have complete data, including sex and total length. Two specimens were missing at least one piece of data and were included for GLG counts but not in other analyses.

Preparation of Sections

At least one tooth was taken from each specimen. A medial longitudinal cut was made on each of the teeth on a Buehler Isomet 11–1180 low speed saw using a rotating diamond blade with a saw speed of 5 to 6 on a relative scale of 1 to 10 (up to 300 rpm), following the method of Hohn (in press). One of the half-sections from each tooth was prepared for scanning electron microscopy. These were soaked in 5% formic acid for 3 hours, rinsed in water for at least one-half hour to remove the acid, cleaned in an ultrasonic cleaner with acetone for 15 to 60 seconds to remove extraneous surface particles, dipped in 70% ethanol to dehydrate and air dried. These etched sections were examined by scanning electron microscopy (SEM) (Hohn, in press). During an SEM session, a standard set of micrographs was taken which included serial micrographs of the entire tooth at low magnification (15 to 20×), requiring up to five micrographs, and higher magnifications (greater than 25×) for difficult to count, narrow GLGs, GLGs bordering the pulp cavity, and possible incremental layers. Specimens were prepared for SEM not more than two or three days before each session to help reduce their absorbing moisture.

For each tooth, a 150 μm thin section was also prepared. In most cases, the cut surface of the remaining half section was glued to a microscope slide and all but 150 μm cut off leaving the thin section adhering to the slide. The thin sections were removed by dissolving the adhesive in acetone, then mounted for examination on a clean slide.

Data Collection and Analysis

GLG counts were made for all of the specimens from the SEM micrographs and from the thin sections using a dissecting microscope with transmitted light (at 25×). The number of GLGs was plotted against total length for each animal. The total length of animals in each of the first 3 age classes (GLGs) was compared for males and females to examine differences in growth rates. The sample sizes were too small for statistical analyses for animals with more than four GLGs.

Measurements for GLG and translucent layer widths were taken for 19 females and 19 males from the thin sections using a dissecting microscope (at 50×) equipped with an ocular micrometer and a polarizing filter. Measurements of the first few GLGs were made near the base of the neonatal line on the concave side of the tooth. In sections in which it was difficult to measure at this point because of unclear boundaries, the GLG width was determined closer to the crown or tip of the tooth. The width of the first GLG is approximately the same from the base of the neonatal line to below the crown so a slight change in position did not affect the measurements. Later layers were measured where they were most clearly defined but in the upper half of the length of the GLG before it becomes compressed in the root, and below the apical end where the layers are especially wide. Sections that did not allow determination of boundaries of adjacent GLGs were not included.

Preliminary examination suggested the growth of the tooth by width of GLGs to be different in males and females. To test this, the width of each GLG was determined for each sex and compared using a Mann-Whitney Rank Sum test. In addition, the ratio of width of the translucent layer to entire GLG was plotted against GLG number, again considering males and females separately.

The optical density and extent of growth of the last GLG were determined and plotted against time of death for 16 males and 12 females whose teeth had fewer than four GLGs. Older animals were excluded because the GLGs become too narrow, and sometimes the boundaries too irregular, to get accurate measurements of a partial layer.

Incremental layers and accessory layers were treated separately. The number of incremental layers per GLG was determined where all of the increments of a GLG could be distinguished. The widths of individual increments were measured by position within different GLGs, i. e., on a ridge or in a groove for GLG 1, 2, or 3, or beyond GLG 3, using the SEM micrographs. The distribution and appearance of irregular accessory layers was noted. For accessory layers that appeared more regularly, their position within the GLG was measured.

Five variables were tested specifically for possible sexual dimorphism related to the neonatal line. First, the extent of the neonatal line beyond the bottom of the enamel was measured in thin sections on the concave and convex side of 42 teeth from mixed males and females. This is similar to the study by van Utrecht (1969). In addition, the width of the prenatal zone at the base of the enamel was determined, also from thin sections on both sides of the tooth. Finally, the width of the translucent neonatal line was compared in females and males. Means for each measurement were compared for males and females using a Student's t-test.

RESULTS

Age and Growth

A scatterplot of 64 females, 54 males and two specimens of unknown sex shows the general growth curve for *Tursiops* from the western North Atlantic Ocean (Fig. 1). For each of the first few age classes, including neonates, and for a cumulative average for animals with more than four GLGs, the mean total length is not significantly different for males and females using a Mann-Whitney test (Table 1). The minimum and maximum total lengths within each age class indicates the large overlap in total length of individuals in different age classes. The decrease in growth,

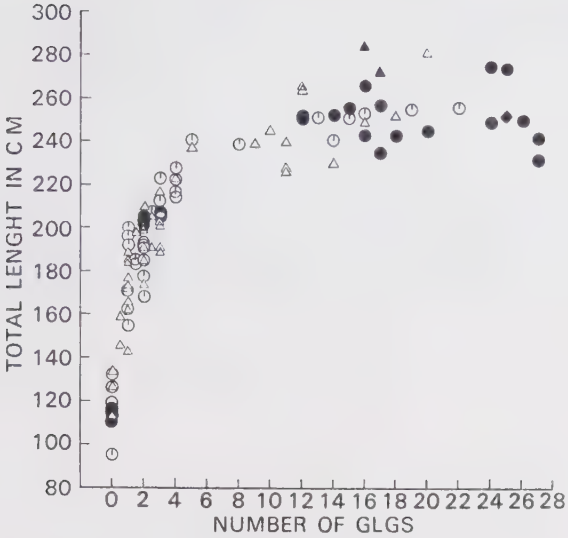

Fig. 1. Scatterplot of the number of growth layer groups (GLGs) to the nearest half-GLG and total length for 120 western North Atlantic Ocean *Tursiops*. Circles are females, triangles are males, diamonds are animals whose sex is unknown. Solid symbols represent a closed pulp cavity.

TABLE 1. SOME DESCRIPTIVE STATISTICS FOR TOTAL LENGTHS OF *TURSIOPS* BY NUMBER OF GLGS AND SEX

No. of GLGs	Sex	N	Total Length (cm)		
			Mean	Min.	Max.
0	F	9	116	95	132
(Neonates)	M	9	118	110	134
0.5	F	0			
	M	2	153	146	159
1	F	6	180	155	200
	M	9	172	143	189
1.5	F	2	184	183	185
	M	1	198		
2	F	11	183	168	205
	M	8	196	174	210
2.5	F	2	207	206	207
	M	1	191		
3	F	6	210	205	223
	M	8	203	189	217
4	F	4	220	214	227
	M	2	220	216	223
More than	F	24	249	232	275
4 GLGs	M	14	250	226	284
	F & M	38	250	226	284

large ranges in total length, and small sample size for animals with more than four GLGs allows for the determination of average "adult" total length of approximately 250 cm.

Description of GLGs

For the most part, GLGs in thin sections of teeth of these *Tursiops* appear as described in other odontocetes, particularly delphinids and *Tursiops* (Sergeant, 1959), as alternating translucent and opaque layers (see Perrin and Myrick, in press). The prenatal zone is a relatively uniform area easily distinguished by its lack of substructure, e. g., incremental and accessory layers, seen in post-natal dentine.

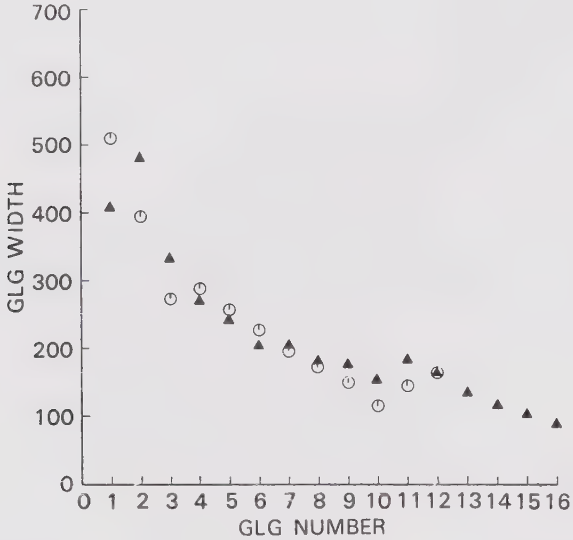

Fig. 2. Average width of GLGs for females (circles) and males (triangles), in micrometers. Measurements based on thin sections of teeth from *Tursiops*.

The neonatal line is a narrow translucent layer usually followed by a narrow, intense opaque layer. The first GLG begins after the neonatal line with a wide, variably opaque layer riddled with accessory layers, and ends with a narrow translucent layer often less apparent than some of the accessory layers. The second GLG is similar to the first in having the wide, variably opaque layer followed by a narrow, relatively, but indistinctly, translucent layer. The third and sometimes fourth GLGs have more distinct opaque and translucent layers and, although accessory layers can still be seen, they are not as overwhelming as in the first two GLGs. Subsequent GLGs have better demarcated opaque and translucent layers, less variability in mineral densities within a layer, and fewer accessory layers.

The same basic description is applicable to etched half-sections where opaque layers are equivalent to grooves and translucent layers are equivalent to ridges.

However, the numerous accessory layers in the first few GLGs are usually not as prominent in the etched sections. The exception is when the mineral density differences, normally accentuated by etching, are small across a GLG (usually in the first two GLGs), then incremental layers and accessory layers in the opaque zone of the GLG are almost indistinguishable from the translucent (boundary) layer of the GLG. This also occurs in thin sections. Furthermore, in etched sections, there are not clear boundaries between GLGs, i.e., there is not an abrupt end to the translucent layer or ridge. Rather, the topography of the surface might be likened to rolling hills with a rounded crest and slopes, and valleys inbetween. This does not allow for clear points or ends of layers from which to make measurements.

In general, the widths of GLGs decrease as the animals get older (Fig. 2). The first few GLGs are the largest and the last few are the smallest (Table 2). More specifically, in females, the first GLG is the widest averaging 509 μm, the

TABLE 2. SUMMARY OF DESCRIPTIVE STATISTICS FOR TOTAL GLG WIDTHS MEASURED FROM THIN SECTIONS OF TEETH FROM *TURSIOPS*. SIGNIFICANT DIFFERENCES DETERMINED USING A MANN-WHITNEY RANK SUM TEST. MEASUREMENTS IN MICROMETERS

GLG No.	Sex	N	Mean Width	Min.	Max.	Significant Differences
1	F	19	509	418	570	$p<.005$
	M	19	407	342	475	
2	F	12	393	285	475	$p<.05$
	M	11	480	380	608	
3	F	6	272	190	342	$p<.05$
	M	10	331	190	418	
4	F	6	285	228	380	
	M	7	269	209	342	
5	F	6	253	171	342	
	M	6	241	152	380	
6	F	6	225	152	285	
	M	6	203	152	266	
7	F	5	194	152	266	
	M	6	203	152	247	
8	F	5	171	95	247	
	M	6	181	133	228	
9	F	5	148	95	228	
	M	6	174	114	228	
10	F	4	114	76	190	
	M	5	152	114	209	
11	F	2	143	114	171	
	M	4	181	133	209	
12	F	2	162	133	190	
	M	4	162	152	190	
13	M	3	133	95	171	
14	M	2	114	95	133	
15	M	4	100	76	135	

TABLE 3. SUMMARY OF DESCRIPTIVE STATISTICS FOR TRANSLUCENT LAYER WIDTH DIVIDED BY GLG WIDTH (=PERCENT TRANSLUCENT LAYER) FOR EACH GLG MEASURED FROM THIN SECTIONS OF TEETH FROM *TURSIOPS*. SIGNIFICANT DIFFERENCES DETERMINED USING A MANN-WHITNEY RANK SUM TEST. RESULTS EXPRESSED AS PERCENTS

GLG No.	Sex	N	Mean Width-%	Min.	Max.	Significant Differences
1	F	19	9	1	17	
	M	19	10	4	14	
2	F	10	15	4	33	
	M	11	14	4	32	
3	F	6	39	18	67	$p<.10$
	M	9	23	5	50	
4	F	6	40	17	60	
	M	6	33	13	50	
5	F	6	41	22	56	
	M	6	41	10	75	
6	F	6	48	33	36	
	M	6	41	14	56	
7	F	5	48	38	58	
	M	6	45	36	50	
8	F	5	50	33	60	
	M	6	49	23	57	
9	F	5	57	40	71	
	M	6	48	33	67	
10	F	4	57	50	67	$p<.10$
	M	6	45	27	56	
11	F	2	73	67	78	$p<.05$
	M	4	44	27	57	
12	F	2	71	70	71	$p<.05$
	M	4	52	38	63	
13	M	3	51	50	52	
14	M	2	47	43	51	
15	M	4	50	50	51	

second is smaller at 393 μm, with subsequent GLGs decreasing in width. An exception is a slight increase in size at GLGs 11 and 12 which might be an artifact of small sample sizes (N=2). In males, the trend is similar except that the second GLG, which is 480 μm, is larger than the first, which is 407 μm. The third GLG is smaller than the first and subsequent GLGs follow the same pattern as in the teeth of females. Again, there is a slight increase in size at GLG 11. Measurements of the widths of GLGs 1, 2 and 3 are statistically significantly different between males and females (Table 2).

The width of the translucent layer follows the opposite pattern. GLGs set down in older animals have wider translucent layers or the width of the translucent layer to the entire GLG (percent translucent layer) increases (Table 3). In females there is a leveling off of percent translucent layer at GLGs 6 through 8, then an increase for subsequent GLGs. In males, the percent translucent layer increases initially, then remains fairly constant after GLG 4. This gives GLGs in the teeth of male *Tursiops* a more even appearance in size and spacing, which is especially apparent in SEM micrographs (Plate I, Fig. 1).

The translucent layer widths between females and males are statistically significantly different at GLGs 1, 3, 6, and 12. The percent translucent layer is significantly different between females and males at GLGs 3, 10, 11, and 12 (Table 3). There are no measurements for females beyond GLG 12.

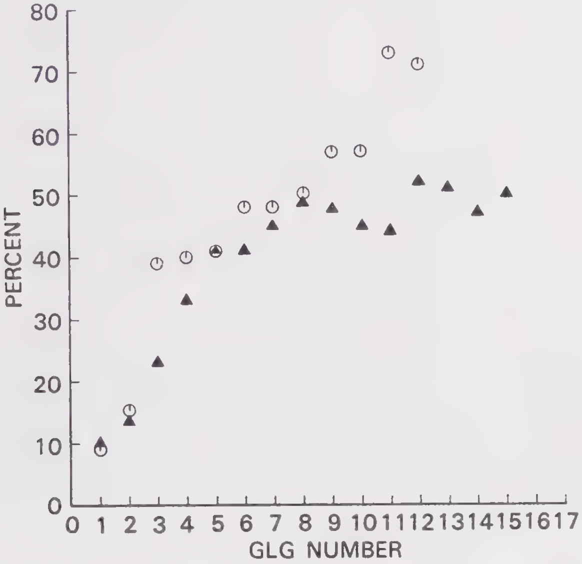

Fig. 3. Average percent translucent layer for each GLG. Circles are females, triangles are males.

Last GLG

A plot of percent growth of the last layer against time of death for 28 female and male *Tursiops* shows most of the points to set roughly on a line representing the expected growth of the current GLG if the deposition of dentine is constant and the new GLG begins in late January or early February (Fig. 4, Table 4). For the cluster of 14 points which occurs during February and March, with four additional points in May, the extent of growth of the GLGs increases proportionally with time along this line. Some of the points which do not fit this line fall on or close to another line representing the expected tooth growth of animals whose new GLG begins in September. However, there are only six specimens representing this group.

In most cases the last layer is opaque (Table 5). The translucent layer borders the pulp cavity in four of the specimens, and one of these is a translucent accessory layer and not a GLG boundary layer. Two of the GLG translucent layers

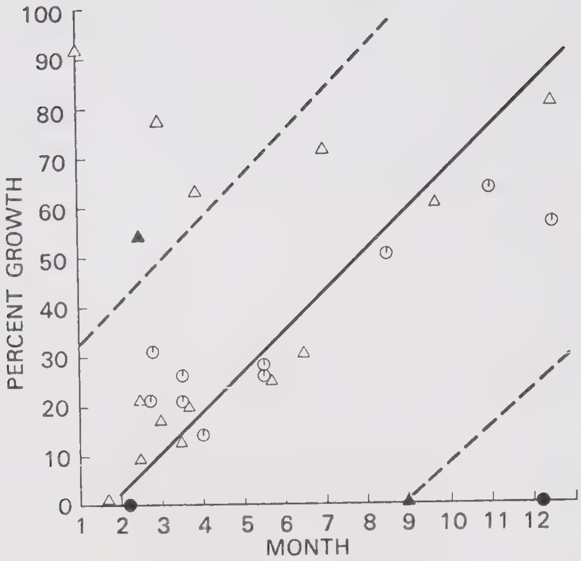

Fig. 4. Scatterplot of the percent growth of the last GLG in teeth of young *Tursiops* on approximate date of death. Percent growth calculated for each animal from actual width of the last layer divided by the average total width of the GLG. Solid line presents expected growth of the GLG throughout the year if the GLG begins in late Jan.-early Feb. and grows at a constant rate. Hatched line represents the same for GLGs which begin in September. Circles are females, triangles are males. Hollow symbols indicate an opaque last layer, solid symbols represent a translucent last layer.

occur in late January to early February and one occurs in September. The accessory layer that falls in mid-March is an animal whose dentinal growth pattern falls on the line for GLGs which begin in the fall.

Non-GLG Layered Structures

In addition to GLGs three layered structures can be differentiated in the teeth of *Tursiops*. Incremental layers are relatively evenly spaced layers which are found throughout the GLGs and are most easily seen in SEM micrographs of etched sections. Accessory layers are layers of opposite mineral density that would be expected within a GLG with an even mineral density. The third structure is similar to an accessory layer because it appears in a layer of opposite mineral density of the dentine adjacent to it.

Incremental layers could be counted and measured from some of the SEM micrographs (Plate I, Fig. 2). The average number of incremental layers per GLG is 11.8 for three GLGs from 39 specimens (Table 5). Of the three GLGs in which incremental layers could fairly consistently be counted, GLG 2 was the easiest for counting. Incremental layers are rarely visible in the compressed GLGs set down

TABLE 4. PERCENT GROWTH OF THE LAST FORMED GLG. GROWTH OF THE LAST GLG AND TIME OF YEAR OF DEATH FOR SOME *TURSIOPS* MALES AND FEMALES. PERCENT LAST LAYER CALCULATED FROM EXPECTED AVERAGE SIZE OF THE FULLY FORMED GLG. OPTICAL DENSITY OF THE DENTINE BORDERING THE PULP CAVITY IS BASED ON THIN SECTIONS USING TRANSMITTED LIGHT

Catalogue No.	No. of Complete GLGs	% Growth Last GLG	Approx. Date of Death	Optical Density
Females				
504565	1	31	late Feb	opaque
504590	1	26	mid-March	opaque
504403	1	26	15 May	opaque
CWP094	1	37	22 May	opaque
SEAN3331	1	50	mid-Aug	opaque
504539	1	56	late Dec	opaque
504550	2	0	early Feb	translucent
504592	2	14	30 March	opaque
504399	2	28	15 May	opaque
504583	2	21	early Mar	opaque
395179	2	63	4 Nov	opaque
504528	2	0	early Dec	translucent
504549	2	21	mid-Feb	opaque
Males				
504578	0	54	late Feb	translucent*
JGM401	0	80	14 Dec	opaque
504536	1	1	21 Jan	opaque
504553	1	9	mid-Feb	opaque
504567	1	21	late Feb	opaque
504218	1	17	1 March	opaque
395790	1	25	22 May	opaque
504535	1	92	early Jan	opaque
504561	2	77	early Mar	opaque
504591	2	25	early Mar	opaque
504290	2	35	mid-June	opaque
504122	2	60	21 Sept	opaque
504551	3	13	11 Feb	opaque
504765	3	13	14 Mar	opaque
CWP084	3	44	late Mar	opaque
504291	3	71	27 June	opaque
504313	3	0	3 Sept	translucent

* translucent accessory layer.

in the teeth of "old" animals, e.g., beyond GLG 10, in etched sections. Even in the first few GLGs incremental layers were not always clear enough to count. On the etched surface of the tooth, they were most clear on the "slopes" rather than on the top of a ridge, where one prominent very wide increment often turned out to be two, or in the grooves, where it is was "dark". The incremental layers have the same three-dimensional pattern as GLGs and are only visible when there is a contrast between the ridges and grooves of adjacent increments.

TABLE 5. NUMBER OF INCREMENTAL LAYERS PER GLG IN *TURSIOPS* DENTINE

Catalogue No.	GLG 1	GLG 2	GLG 3	>3 GLGs
291472	12–13	12	12	10–11
504122	9	13	—	—
291431	12	11	13	8-9
291403	—	12	10	11-12
291402	—	13	—	9
12277	—	11	—	—
291462	12	11	—	—
CWP088	—	—	—	11 11
191456	14	—	—	9
504534	14	12	12	—
504864	12–13	—	11–12	—
504726	—	11	10	—
291498	—	11	10	10–12
291466	—	—	11–12	—
395430	—	—	—	10
395179	12	—	—	—
504561	—	11	—	—
JGM399	11	—	—	—
291426	—	15	11	—
		Summary		
Means	12.2	11.8	11.3	10.8
Std. dev.	1.6	1.2	1.1	1.2

The widths of the incremental layers varied slightly (Table 6). Their mean width in GLG 1 was 26 μm and 23 μm, for ridges and grooves, respectively, 28 μm and 26 μm in GLG 2, 27 μm and 24 μm in GLG 3, and 23 μm and 20 μm for measurements made from GLGs later than three. It appears, in general, that increments in the grooves are smaller than those on the ridges in the same GLG and that the increments become smaller with successive GLGs.

Conversely, accessory layers tend to be variable in position and intensity, but are usually thin translucent layers or lines within the opaque layer of the GLG. In addition, in each of the first two GLGs there is an especially wide, prominent layer about halfway through the GLG (Plate II, Fig. 1). In the first GLG, this accessory layer occurs an average of 50% through the GLG in females and 64% of the width of the GLG in males. It occurs approximately in the middle of the second GLG in females and males. In some teeth these accessory layers are more conspicuous than the GLG boundary layer. This is particularly true since in the first two GLGs the translucent boundary layer is very narrow. In GLGs beyond number three, accessory layers become less frequent and the center, wide accessory layer is not as pronounced. Accessory layers are not found in the compressed GLGs set down in old animals.

A third non-GLG layered structure might also be called an accessory layer. These layers occur adjacent to any accessory or GLG boundary layer as very in-

TABLE 6. WIDTHS OF INCREMENTAL LAYERS IN *TURSIOPS* DENTINE MEASURED FROM SEM MICROGRAPHS OF ETCHED SECTIONS. MEASUREMENTS ARE SEPARATED BY THEIR LOCATION WITHIN A GLG AND BY GLG NUMBER. MEASUREMENTS IN MICROMETERS

Catal. No.	GLG 1		GLG 2		GLG 3		>3 GLGs	
	Ridge	Groove	Ridge	Groove	Ridge	Groove	Ridge	Groove
291472	38.8	35.4	34.6	28.9	25.4	26.6	20.3	—
504122	29.8	20.0	26.0	24.0	—	—	—	—
291431	34.5	25.0	—	31.8	—	36.3	23.9	—
291403	—	—	27.5	25.0	—	—	—	17.5
291402	—	—	25.8	20.0	—	—	25.0	22.8
12277	—	—	32.0	30.0	32.5	22.5	—	—
291462	29.3	32.5	31.5	—	—	—	—	—
CWP088	—	—	—	—	—	—	30.8	—
							16.8	—
291456	—	—	—	—	—	—	20.3	—
504534	22.1	18.9	19.8	—	—	17.1	—	—
504864	22.5	15.0	20.3	20.2	—	16.7	—	—
504726	—	—	—	35.7	28.6	—	16.3	—
291498	—	—	18.4	15.2	18.0	—	—	—
291475	—	—	31.0	22.8	—	—	—	—
291466	—	—	—	—	40.0	20.0	26.6	—
395179	14.3	11.9	—	—	15.1	—	—	—
504561	—	20.0	14.4	—	—	—	—	—
JGM399	—	28.6	47.7	28.6	—	—	—	—
504532	—	—	29.9	29.2	—	—	27.8	—
291426	31.3	—	—	29.8	—	28.0	22.5	—
395430	—	—	20.0	—	—	—	—	—
				Summary				
Means	26.2	23.4	27.6	26.2	26.6	23.9	23.0	20.2
Std. Dev.	7.5	8.4	8.7	5.7	9.2	7.0	4.7	—
Overall mean		26.1						
Std. Dev.		7.0						

tense narrow bands of the opposite mineral density as the structure they abutt. Most often, this layer is opaque and follows a translucent layer. It is very noticeable following the neonatal line, the wide central accessory layer, and some of the irregular accessory layers throughout the GLGs. When this structure occurs by thin translucent boundary layers, it is sometimes more prominent than the translucent layer so more easily used as the boundary layer (Plate II, Fig. 2).

Sexual Dimorphism

Measurements of four of the five variables specifically tested for possible sexual dimorphism similar to that found by van Utrecht (1969) proved not to be significantly different (Table 7). The difference in the fifth variable, neonatal line width, was highly significant ($p<.005$) using a t-test with males having a wider neonatal line than females.

TABLE 7. SUMMARY OF MEASUREMENTS FOR POSSIBLE SEXUAL DIMORPHISMS IN THE TEETH OF *TURSIOPS*. MEASUREMENTS IN MICROMETERS

Variable	Sex	N	Mean	S. E.
Extent neonatal line extends beyond enamel, convex side*	F	13	418.0	64.2
	M	18	471.8	52.5
Extent neonatal line extends beyond enamel, concave side*	F	17	429.2	54.4
	M	18	405.3	53.3
Width of prenatal zone, convex side*	F	13	58.5	4.4
	M	18	54.4	4.3
Width of prenatal zone, concave side*	F	16	54.6	5.2
	M	18	48.1	4.6
Neonatal line width convex side**	F	21	27.0	0.8
	M	22	37.3	1.3

* Not significantly different using Student's t-test.
** Significant at $p<.005$.

DISCUSSION

Age and Growth

The growth rate of *Tursiops* is similar to that of many other odontocetes. During its first year, an average western North Atlantic *Tursiops* increases its length by 53%, approximately the same increase found for the same age animals of *Stenella attenuata* (Perrin *et al.*, 1976), *S. coeruleoalba* (Kasuya, 1972, 1976), *Globicephala melaena* (Sergeant, 1962), *Tursiops* from Florida (Sergeant *et al.*, 1973), and *Tursiops* from South Africa (Ross, 1977). The rate of growth decreased during the second year of life, averaging only a 10% increase in total length in these *Tursiops* and an average of 10 to 15% in the other species mentioned above. After three GLGs the growth rate slows considerably.

Cetaceans have been described as having high rates of growth while they are young (Bryden, 1972). However, there is a great deal of variability in total lengths of individuals in any age class. In *S. longirostris*, animals with one GLG range from about 100 cm to 135 cm in total length, those with two GLGs range from 110 to 145 cm, with equivalently large variation in older animals (Perrin *et al.*, 1977). In pilot whales, *G. melaena*, neonates range from 165 to 195 cm in total length (Sergeant, 1962). A sample of harbor porpoises from the Bay of Fundy ranged from 75 to 105 cm at birth, 105 to 130 cm at one year, 118 to 135 cm at two years, 125 to 145 cm at three years, again continuing this variation in length within each age category for older animals (Gaskin and Blair, 1977). The large variability and overlap of different aged animals illustrates that, although it is useful to construct growth curves and use mean total lengths for examining growth rates, it is not reliable to use total length to determine the age of an individual.

In the western North Atlantic *Tursiops* an especially large range in total length exists in each age class. This may be due to strandings of individuals from two different population of *Tursiops*, coastal and offshore, where the offshore animals seem to be larger than those found along the coast (J. G. Mead, unpub. data). At this time, however, it is not possible to differentiate to which population a young stranded animal belonged, so all specimens less than 280 cm have been included.

Differences in adult total length or rate of growth between males and females have been found in some cetaceans. When it occurs, generally males are larger than females as adults in odontocetes (e.g. pilot whales and sperm whales), while in mysticetes males are smaller than females as adults (e.g. humpbacks and fin whales) (Bryden, 1972). But delphinids generally have not been found to be dimorphic in adult total length (True, 1889; Sergeant *et al.*, 1973). The results from this study seem to support this.

Two studies have been published on the growth rate of wild *Tursiops*. Sergeant *et al.* (1973) looked at *Tursiops* from Florida waters. Although they reported birth to occur at 100 cm, they present no data for neonates. The growth curve, based on 22 males and 24 females, is similar to that of western North Atlantic *Tursiops* but with younger animals (less than five GLGs) apparently smaller in Florida. The apparent difference between the two groups may be due to differences in our definition of GLGs. The asymtotic length of males from Florida was found to be 270 cm and that of females to be 250 cm. The coastal *Tursiops* in this study appear to have the same asymptotic length for males and females at 250 to 260 cm. Ross (1977) gives some biology of *T. aduncas* from South African waters. The age of birth ranged from about 84 cm to 112 cm. Females reached sexual maturity at a smaller length than males. The largest female was 252 cm and the largest male 254 cm which makes them smaller than the western North Atlantic *Tursiops*. Although the *Tursiops* from Florida waters might be the same type as those from further north along the coast, those from Africa are probably not.

GLG Widths

As a dolphin tooth grows and deposits more dentine, the pulp cavity becomes increasingly smaller until it finally occludes and no more dentine deposition can occur. Correspondingly, as the pulp cavity becomes smaller, the GLGs become narrower. This decrease in GLG width could be solely the result of the new forming GLG being compressed into a smaller pulp area. If this is the case then each GLG would be a little smaller than its preceding GLG and a plot of the relationship between GLG width and number would be approximately a straight line with a negative slope. If this relationship follows a different pattern then it would suggest that there are other factors influencing the deposition or mineralization of dentine.

There are some general patterns that can be found in a plot of average GLG width against GLG number that suggest that physiological factors affected by the age or sex of the animals are important in GLG growth. These patterns can be visualized in Fig. 2. First, there are significant differences between males and females in the widths of the first two or three GLGs. It is particularly interesting that the second GLG is, on the average, wider than the first GLG in teeth from males, and that the third GLG decreases so that it is narrower than the first. Secondly, the changes in width of the first three GLGs is large, but subsequent GLGs show a marked decrease in this rate, i.e., GLGs following number three are not much narrower than their adjacent preceding GLG. This appears to be an affect of age of the animals since it occurs in females and males. Again it is interesting that this abrupt decrease in GLG deposition rate occurs at the same time that the growth curve of *Tursiops* (Fig. 1) shows a noticeable decrease in rate of growth. Thirdly, the average width of each GLG is larger in females than in males from GLGs four to six and smaller in GLGs which follow. The effect is an almost constant decrease in width of GLGs four through ten in females. In males, the rate of change in width of GLGs appears smaller than in females for GLGs six through ten. In an etched section of tooth, these GLGs appear evenly spaced and sized across the surface and almost can be considered diagnostic to determine teeth from males. Similarly, the characteristic constant decrease in size of GLGs in teeth from females is apparent in etched sections. Perrin *et al.* (1977) plotted the percent decrease in width from one GLG to its adjacent GLG in the spinner dolphin beginning at GLG 3 and continuing to GLG 16. They found that each GLG average more than 95% of the width of the preceding GLG. They did not consider females and males separately, which in *Tursiops* teeth gives different results, as discussed above. A progressive decrease in width of GLGs has also been described from the harbor porpoise (Nielsen, 1972; Gaskin and Blair, 1977), striped dolphin (Kasuya, 1972), and the pilot whale (Sergeant, 1962). Christensen (1973) found an initial decrease in bottlenose whales followed by constant thickness after the fourth GLG. Except for Gaskin and Blair (1977), measurements of widths were not given, nor were specific differences by sex or age noted. The mean widths of GLGs given by Gaskin and Blair (1977) show that GLGs are wider in teeth from female harbor porpoises than those from males.

The translucent layer can also be used as an indicator of physiological changes affecting GLGs. The absolute value of the width of the translucent layer is probably not an important parameter by itself, except to help determine the time span over which it is deposited, because it is dependent on the GLG number and width. The percent translucent layer is a more useful quantity. As with GLG width, the trend in percent translucent layer is different in females and males although significant differences occur only in GLGs 3 and 10 through 12. In females, the percent translucent layer increases almost continuously with age. Beyond GLG 10 more than half of the GLG consists of the translucent layer, reaching about 70%. This trend appears as an initial rapid increase in percent translucent layer which levels almost as a plateau (between GLGs 3 through 8) then increases rapidly again after GLG 8. This is noticeably different than males where an initial rapid increase in percent translucent layer leads to a nearly constant level, with some fluctuation. The translucent layer comprises only about 50% of the GLG after GLG 8. The change in percent translucent layer around GLG 8 through 10 in females and males may be related to physiological changes associated with the onset of sexual maturity, since this seems to be approximately the age at which the animals become sexually mature (Harrison, 1969; Ridgway, 1972).

The changes at GLGs 3 to 4 may be influenced by the decreasing growth rate at that age. The large percent translucent layer in females beyond age ten can be speculated about with even less certainty. The most obvious explanation since there are such large differences between males and females would be that the wide translucent layer, which is hypomineralized (Hohn, in press), is the result of a calcium drain caused by reproduction. At this time, there is no direct evidence for this. Gaskin and Blair (1977) noticed a progressive increase in proportional thickness of the translucent layer with age in harbor porpoises but only in females, so they attributed it to calcium mobilization. They constructed a regression line through a scatterplot of the proportion of opaque layer to translucent layer but did not mention specific differences at any age. However, their results, along with mine, indicate that percent translucent layer is worth examining in other species for possible dimorphism and explanation for the formation of the layers.

Last GLG

Most of the strandings of *Tursiops* occurs during February and March. Since calving also occurs during this season, it should be about this time when the neonatal line appears in the teeth. If the deposition of dentine is fairly constant, animals born in the late winter to early spring would have completed each GLG during that season in successive years and then started another GLG. Each month more of the new GLG would have accumulated following a hypothetical line representing constant growth by percent GLG formed throughout the year, one twelfth or 8% monthly, as in Fig. 4. Most of the 28 animals examined for percent growth of the last GLG follow this hypothetical line, at least during the spring of the year when most of the animals strand. However, this line begins in January or early February, earlier than when neonates are generally found. By late February or March, 10 to 20% of the new GLG has already formed, the amount that would be expected at a constant deposition rate of dentine with the new GLG beginning in January. This would suggest that the end of the previous GLG, which is the translucent layer, occurs in December or January. Scatter around this line is probably due to individual variation in time of birth and actual widths of GLGs, and possibly to abnormal physiological states of the animals before they strand.

Tursiops may have two seasons of parity: one in the spring and another in the fall (Townsend, 1914; Harrison, 1969; Ridgway, 1972; Ross, 1977). In particular, Townsend (1914) believed that North Atlantic Ocean *Tursiops* give birth during both seasons. Ross (1977) has found stranded neonates in the fall and spring which suggests more than one or an extended breeding season. But neonates have not been found through the MMSP during the fall, even though many are picked up during the spring. However, if the growth of the tooth can be used as an indicator of season of birth, i.e., animals born in the spring have formed one GLG the following spring as previously discussed, then *Tursiops* which have formed 50% of a GLG in the spring must have started that GLG during the fall. Similarly, an animal whose last GLG ends in the fall, probably also began deposition of GLGs during the fall. A hypothetical line drawn to represent the expected growth of teeth which begin GLGs in the fall should parallel the equivalent line for animals whose GLGs begin in the spring, but off-set by approximately six months. This hypothetical line, represented in Fig. 2, has several points which fall on or close to it. This would suggest that these animals were also born in the fall rather than in the spring as we would have anticipated based on stranding records. This may provide evidence to support Townsend's (1914) idea of two seasons of calving for *Tursiops* in the North Atlantic Ocean.

Although growth layers in teeth and bone have been used for about 30 years for age determination, there have been only speculative suggestions as to the cause of the rhythmic deposition of the layers. The environmental or endocrinological mechanisms influencing or regulating the mineralization pattern in hard tissue is unknown. In several species of odontocetes, the optical or mineral density of the GLG layer bordering the pulp cavity when an animal dies has been used as an indicator of the physiological or nutritional state of the animal. Sergeant (1959) found the "clear zone" (translucent layer) to begin in February and occur through April in captive *Tursiops* from Florida. Sergeant *et al*. (1973) said they could not determine the density of the last layer in mostly wild *Tursiops* from Florida based on their sample size (N=62). Sergeant (1962) found the opaque zone to occur adjacent to the pulp cavity in pilot whales, *Globicephala melaena*, from Canadian waters caught in the summer. In a mass stranding of pilot whales, *G. macrorhynchus*, in South Carolina during mid-October, the opaque layer bordered the pulp cavity (unpub. data). Nishiwaki and Yagi (1954) found that the well stained (=opaque) layers occur in December and May through June in *S. coeruleoalba*. Similarly, the opaque layer borders the pulp cavity in June through February in harbor porpoises from the Bay of Fundy (Gaskin and Blair, 1977), in the summer in Baird's beaked whales from the North Pacific (Kasuya, 1977), in May and June in bottlenose whales from the North Atlantic (Christensen, 1973), and in June through November in dugongs from the equatorial and North Pacific (Kasuya-and Nishiwaki, 1978). In summary, the opaque layer appears to border the pulp cavity at least during the summer months, and usually longer, in most species. Conversely, the translucent layer is more often at that point during the winter or early spring. In *Tursiops*, the translucent layers, as accessory layers or GLG boundary layers, are deposited in the fall (September, N=1), and in late January, early February, or March (N=3). However, all the animals examined were young which is when the translucent layer is very narrow. As males and females age, a higher proportion of each layer becomes translucent, so the time of deposition of each layer of a GLG would depend on the age of the animal, at least in *Tursiops*. This, again, assumes that the dentine continues to be deposited at a constant rate and only the mineralization pattern changes. The GLG number at which previous researchers determined the optical or mineral density of the layer bordering the pulp cavity, or changes in the relative amount of translucent dentine, has not been mentioned. The collection of enough data of this kind may help us to understand the cause of layering.

Non-GLG Layered Structures

Incremental layers. It is difficult to count incremental layers from SEM micrographs because the small mineral changes throughout an increment and between increments does not always produce enough contrast in etched sections to make individual increments clear (Plate III). In addition, increments are difficult to see on the "back side" of a ridge or in a groove where it is "dark" because fewer electrons reach the collecting plate. The effect is probably that counts are slight underestimates of actual numbers of incremental layers.

Partially for the same reasons, it may not be accurate to measure widths of incremental layers from etched sections. The etching process produces the ridge and groove pattern in GLGs and in incremental layers, so there is no longer a flat surface. This is compounded by the tilting of the sections in the SEM chamber. Although the quantitative effect of these factors is unknown, the average number of increments per GLG (12) multiplied by the average width of the increments (26 μm) is not equivalent to the average width of the first three GLGs measured from thin sections (approximately 420 μm). Measurements are probably an underestimate of actual sizes of increments. SEM of etched sections, however, seems to provide the best way to visualize incremental layers.

The appearance of incremental layers in *Tursiops* dentine supports the idea of Schour and others that dentine grows or is mineralized in spurts or increments. The frequency of approximately 12 increments in one annular layer or GLG suggests that this sub-annual growth is similar to that described in dugongs (Kasuya and Nishiwaki, 1978), Baird's beaked whale (Kasuya, 1977), and dolphins of the genus *Stenella* (Myrick, in press). However, the width of the increments has not been determined for those species. The average size (26 μm) of incremental layers in *Tursiops* dentine seems much too large to represent daily von Ebner's lines of 5 μm width described by Krauss and Jordan (1965) and Newman and Poole (1974) in human teeth, or von Ebner's lines in pig dentine (Yilmaz, Newman, and Poole, 1977). If incremental lines in *Tursiops* are approximately monthly, daily increments would have to average 0.87 μm, measured from SEM micrographs. Myrick (in press) has found daily increments in dolphin dentine, but has not determined the width of either these von Ebner's lines or the "monthly" growth increments. Schour and Hoffman (1939) measured the "calcification" rhythm in 17 species of vertebrates and found it to recur at intervals of 16 μm (no time interval was mentioned). They were counting accentuations (light or more calcified areas) which alternated with dark areas. It is possible that "monthly" increments in *Tursiops*, which are the result of mineral differences, are similar to the pattern found in other vertebrates by Schour and Hoffman (1939).

One of two basic assumptions seems to be made when considering the deposition or mineralization of dentine. The first presumes the increments are time-regulated by some extrinsic or intrinsic factor so that the common denominator is the number of increments set down during a given period of time. The second assumption is that these processes continue at a constant rate regardless of the age or the species of the animals. The latter would seems to be supported by Schour and Hoffman's (1939) observations of the 16 μm calcification rhythm and researchers looking at constant sizes of von Ebner's lines (Krauss and Jordon, 1965; Newman and Poole, 1974). However, the authors do not specify the age of the dentine where the measurements were made, e.g., immediately subjacent to the enamel or several years growth away from the enamel. Nor do they mention making a series of measurements throughout each tooth, except over short periods of time such as days or weeks. Although my measurements of incremental layers are subject to error, as discussed previously, the trends suggest that the increments decrease in size in GLGs set down later in an animal's life. Increments in GLGs beyond number three are smaller than those in the first three GLGs. This may be an artifact of etched sections. However, in order for the number of increments to remain the same in all of the GLGs, the increments must become narrower as the GLGs become narrower; again with the assumption that the number of incremental layers is relatively constant, which seems to be more supported by the data from *Tursiops* teeth.

The assumption of constant size of increments also seems to be disputed by the differences in width of incremental layers on the ridges and grooves in etched sections. Increments in the grooves measure, on average, smaller than increments on the ridges and slopes of the GLGs. This size difference may be a result of the collapse of the tissue when the mineral is removed or it may be a real difference in widths of increments in the hypomineralized and hypermineralized parts of the GLG. This should be checked in untreated dentine, possibly in thin sections using a petrographic microscope (Myrick, in press).

It is tenable that the mineralization or deposition of dentine could be regulated by monthly or lunar factors, that this produces the relatively constant number of increments per GLG in *Tursiops* teeth and possibly all species, that the size of the increments changes progressively with the age of the animal and possibly between the hypo- and hypermineralized layers of the GLGs, and that the incremental layers can be used to gain more information about the biology of species and the growth of mineralized tissue. However, this must be measured by direct marking of individuals, e.g., tetracycline, or by the examination of many more species before any conclusions are drawn.

Accessory layers. There appears to be two kinds of accessory layers as they have been described formally or referred to in the literature. The first are the narrow accessory layers which appear irregularly in GLGs. These are approximately the same size as incremental layers and can be distinguished from incremental layers only because their mineral density, seen as optical density, differs appreciably from that of the GLG layer in which they occur. The second kind are the very prominent, wider than incremental layer accessory layers which occur regularly, approximately in the center of the GLG. It is undoubtedly these prominent accessory layers which are responsible for the debate about number of GLGs set down annually in odontocete teeth. An unexperienced person would almost assuredly count these regular accessory layers as GLGs. For example, Leatherwood *et al.* (1978) counted five GLGs in thin sections of teeth from a young *Tursiops* (USNM 504122). In the same animal I counted a little more than two GLGs (Plate 5). The SEM micrograph shows only two GLGs (although the first prominent ridge is an accessory layer - the first translucent layer is hardly visible). Similarly all of their counts of GLGs from seven *Tursiops* used in both studies are in disagreement with mine, with their counts from the teeth of young animals doubling mine. Kleinenberg and Klevezal (from Klevezal and Kleinenberg, 1967) described an annual deposition of two GLGs in the teeth of the Black Sea dolphin, *Delphinus delphis*, which they later (1967) attributed to the presence of this accessory layer. In general, they agreed that GLGs are annual but this prominent center accessory layer often gives the impression that two GLGs are deposited.

Myrick (in press) refers to incremental layers in *Stenella* teeth as accessory layers. It seems that incremental layers are visible due to their mineralization cycle within GLGs. If this cycle is subject to extrinsic or intrinsic influences then incremental layers will be more obvious within a GLG when the expected mineral density is disrupted. This disruption would make the incremental layer appear as one of the narrow, irregular accessory layers. In the first two GLGs where the translucent layer is very narrow, these accessory layers would and do make it difficult to determine where the GLG ends. However, incremental layers by themselves do not usually interfere in the process of counting GLGs in *Tursiops* teeth, especially using SEM.

Regardless of the kind of accessory layer, accessory layers make counting GLGs very confusing in the first few GLGs. A person experienced in "reading" odontocete teeth can probably estimate very close to the actual number of GLGs in a tooth section, but identifying the exact end of a GLG becomes very difficult in some teeth. There is also a great deal of variability between animals. Accurate age determination of some species of odontocetes, e.g. *Tursiops*, depends on experience, from looking at many teeth from all ages of the animals to accurately identify accessory layers before trying to count GLGs.

Small scale mineral changes. The narrow opaque accessory-type layers which follow translucent layers appear to be the result of abrupt small-scale changes in the dentine. Irving and Weinmann (1948) described a similar occurrence in rat incisors. They injected rats with strontium to observe the effects on calcification in the teeth and found that the strontium caused a hypocalcified layer (16 μm wide) to occur. Immediately following this layer, a very evident narrow "calciotraumatic" line was found which sharply demarcated the hypocalcified dentine from the normal, calcified dentine. They attributed this line to be caused by a shock to calcium metabolism in the rat by the strontium. The same effect was found in rats after administration of calciferol or parathyroid hormone (Schour and Ham, 1934; Schour *et al.*, 1934), or immediately following parathyroidectomy (Schour *et al.*, 1937), where the parathyroid helps regulate mineralization processes. In addition, Kronfeld and Schour (1939) found the calciotraumatic line to occur following the neonatal line. It may be this same calciotraumatic line that is present in thin sections of *Tursiops* teeth following the neonatal line and other translucent zones.

There has been some question about the mineral density of the narrow layers in odontocete teeth, for example, the neonatal line. The consensus is that they are translucent and hypomineralized. But Nielsen (1972), Klevezal and Kleinenberg (1967), and Kasuya (1976) have suggested that the narrow layers are translucent but hypermineralized for some species. The wide layers are then relatively hypomineralized, so the relationship between mineral and optical densities is different from that of other odontocetes. Because of this, Nielsen (1972) has suggested that optical density cannot be used as an indicator of mineral density. However, it may be that where the translucent layer is very narrow, the opaque "calciotraumatic" line is more apparent and is considered the layer. In some tooth sections of *Tursiops* it is easier to use this opaque line than the preceding translucent layer to follow a GLG down the extent of the tooth. However, the neonatal is still considered to be translucent and hypomineralized and subsequent boundary layers are translucent and hypomineralized. The calciotraumatic line needs more examination for its occurrence and effect in odontocete teeth.

Sexual Dimorphisms

The sexually dimorphic trait found by van Utrecht (1969), i.e. the greater extent of the neonatal line in males, in teeth from 20 harbor porpoises, *Phocoena phocoena*, is not significantly different in the teeth of male and female *Tursiops*. Van Utrecht also mentioned that the same trait was applicable to *Lagenorhynchus albirostris*, a delphinid, but this was based on only three females and three males. Teeth of species from the family Phocoenidae are considerably different from those of the family Delphinidae. Instead of the nested "cone" appearance of GLGs in *Tursiops* teeth, the GLGs in *Phocoena* are bulbous in the crown or spatulate end, then continue in the narrower root parallel to the long axis, as in the handle of a spatula. The difference in growth between phocoenid teeth and delphinid teeth presumably allows for any dimorphic growth of the neonatal line relative to the top of the cement in *Phocoena* but not in *Tursiops*.

The second trait examined for possible differences between sexes of *Tursiops* seems related to the first. If the neonatal line was to extend further down the root of the tooth in male *Tursiops* as it does in male *Phocoena*, it might be because there was a greater amount of prenatal dentine in males. Having more prenatal dentine could have suggested that the neonatal line was deposited at a later time in males or that the tooth began development earlier. But neither trait was significant so should not be used to identify an animal of unknown sex in *Tursiops*.

The greater extent of the neonatal line could also be related to the width of the neonatal line. If the measurements were made from the outer edge of the neonatal line, a wider neonatal line would extend its length if the deposition of the neonatal line was initiated at the same time in males and females. In the case of *Tursiops*, the width of the neonatal line is significantly different in males and females. However, the greater neonatal line width in males is coupled with insignificant differences in either the extent of the neonatal line or width of the prenatal zone. This is probably because the neonatal line is very narrow, especially relative to its length, and the 10 μm mean difference in this width between males and females does not significantly alter the overall measurement of the extent of the neonatal line. In addition, it is very difficult to accurately measure the neonatal line width because it is so small and, although not difficult to identify, its boundaries are not always clear. Even though the width of the neonatal line proved to be a significantly different sexually dimorphic trait, I would not recommend that it be used as the sole identifier of the sex of an unknown specimen of *Tursiops*.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. SEM micrograph of etched longitudinal section of tooth from an old male *Tursiops* showing relative evenness in GLG width, translucent layer width, and spacing of GLGs. Magnification: ×17.

Fig. 2. Etched longitudinal section of tooth from a 2.5 year old male *Tursiops*. The small layers running parallel to the GLGs are incremental layers. Although more than two GLGs are present, the first is deceptively masked so that the actual boundary layer, marked by the arrow, is not the first prominent ridge. The beginning of the second prominent ridge serves as the boundary for GLG 2. nl neonatal line, al—accessory layer, PC– pulp cavity
Original magnification: ×18.

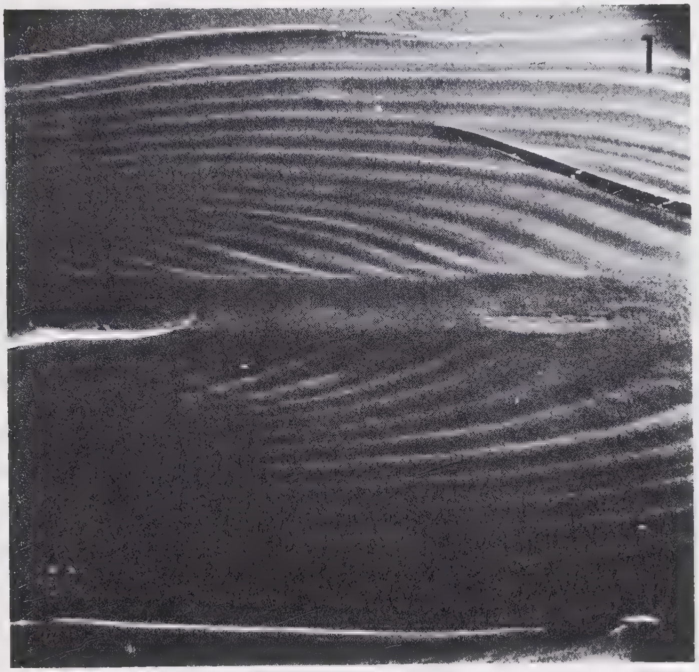
PLATE II

Fig. 1. Longitudinal thin section (transmitted light) of a young *Tursiops* tooth. The dark evident line following the neonatal line (nl) may be a "calciotraumatic line". One GLG is complete, the second is beginning. The center accessory layer (al) is very evident and could easily be mistaken for an additional GLG.
Magnification: ×18.

Fig. 2. Longitudinal thin section of a tooth from a male which could have from 1.5 to 6 GLGs. This animal is probably just over 3 three years old. The GLGs are marked by arrows. Notice the accessory layers which occur centrally in the first two GLGs.
nl—neonatal line
Magnification: ×12.

PLATE III

Fig. 1. Etched section of same 2.5 year old male in Plate II, Fig. 2 at a higher magnification. Notice especially that it is difficult to separate individual incremental layers (il) because two adjacent layers with small mineral density differences appear as one.
nl—neonatal line, al—accessory layer
Magnification: ×50.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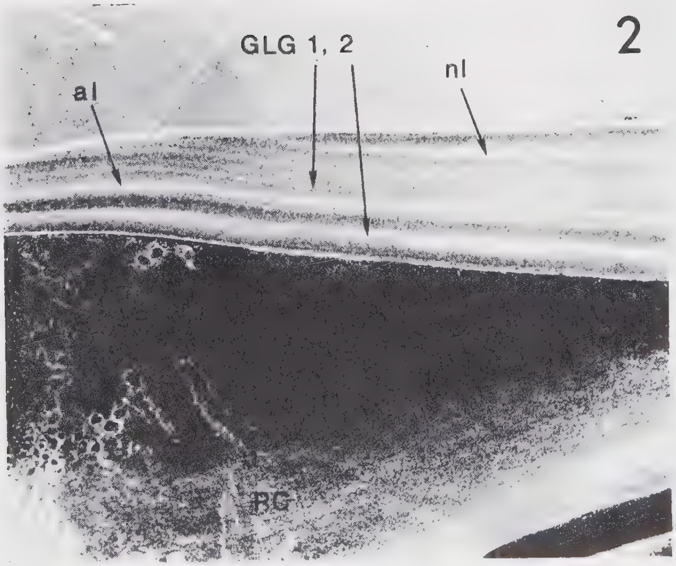
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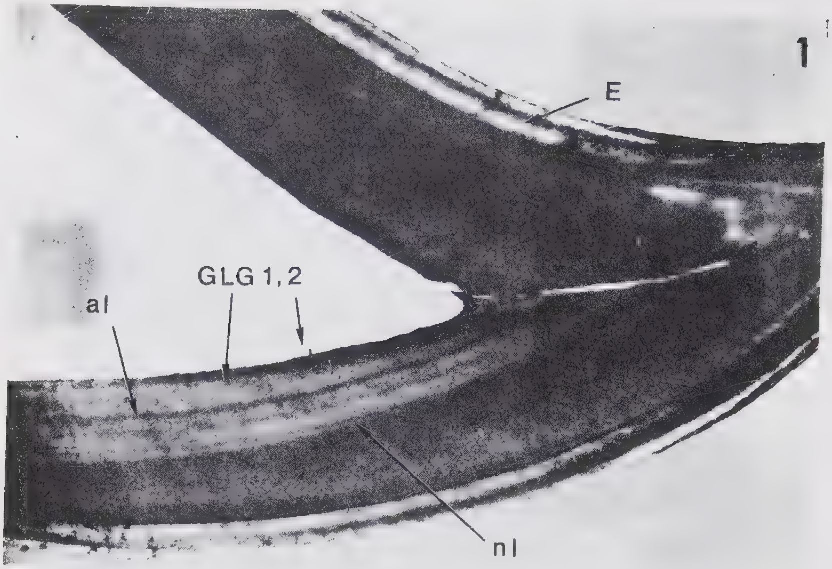
GLG 1, 2
al
nl
BG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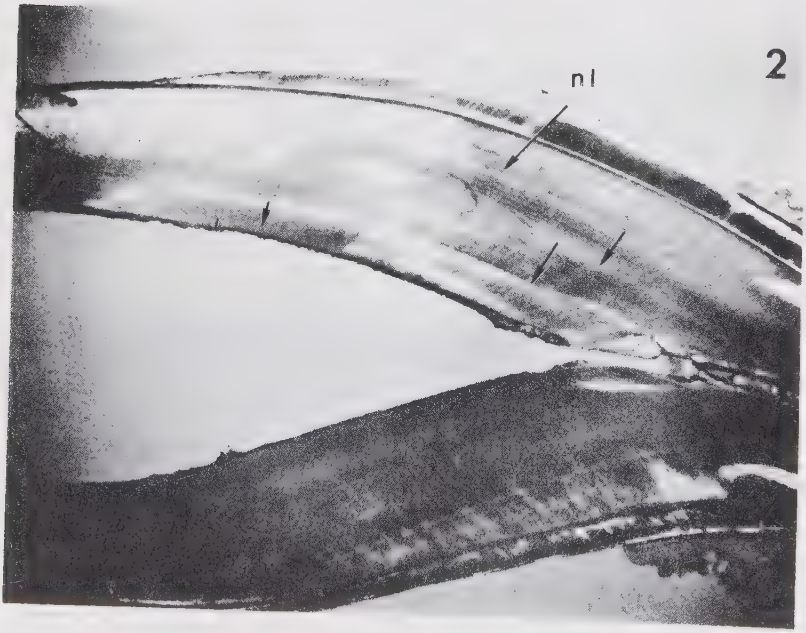
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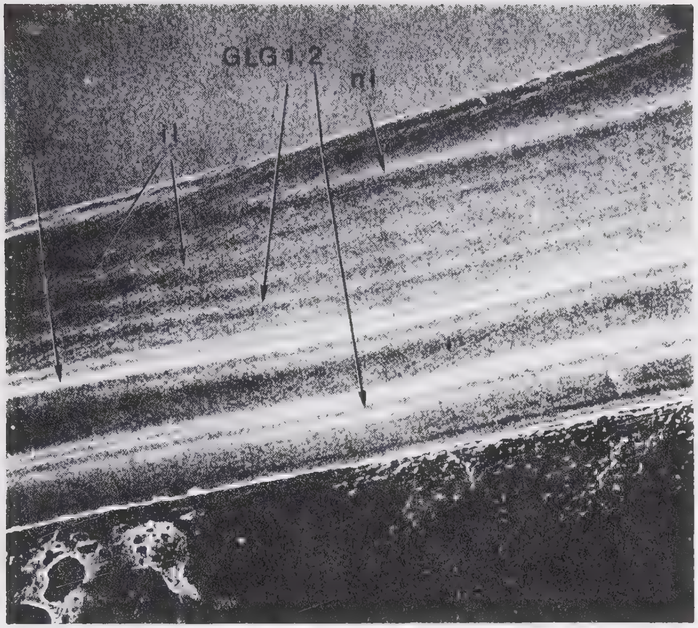
GLG1,2
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8027

Analysis of Growth Layers in the Teeth of *Tursiops truncatus* using Light Microscopy, Microradiography, and SEM

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ABSTRACT

Preliminary results show microradiography and scanning electron microscopy (SEM) to be more accurate methods of accessing growth layer groups (GLGs) in the teeth of *Tursiops truncatus* than transmitted light microscopy. Microradiography shows the rhythmic deposition of mineral as alternating radiopaque and radiolucent layers. It improves the resolution of GLGs near the pulp cavity in older individuals, better than either SEM or light microscopy. SEM of etched sections show GLGs as ridges and grooves which are easily counted from the micrograph. SEM also shows GLGs to be composed of fine incremental layers of uniform size and number which may allow for more precise age determination. Accessory layers are usually hypomineralized layers within the hyperminerailzed layer of the GLG and are more readily distinguishable as such in SEM of etched sections and microradiographs than in thin sections viewed under transmitted light. The neonatal line is hypomineralized, appearing translucent under transmitted light, radiolucent in a microradiograph, and as a ridge in SEM.

INTRODUCTION

Conventional methods of counting growth layer groups (GLGs) in odontocete teeth, by use of undecalcified or decalcified and stained thin sections, have been used extensively in age determination (for example, Nishiwaki and Yagi, 1953; Sergeant, 1959, 1962, 1973; Klevezal' and Kleinenberg, 1967; Best, 1970, 1976; Christensen, 1973; Kasuya, 1972, 1976, 1977; Sergeant, Caldwell, and Caldwell, 1973) but do not always permit definition of all GLGs. Repeated counts on the same tooth by one person or several people sometimes give different results with the average or median count used as the age indicator (this workshop; Kasuya, Miyazaki, and Dawbin, 1974; Perrin, 1975; Kasuya, 1977). The development of a technique that will lead to better resolution of GLGs, and therefore more accurate age determination, would be useful. Preliminary work with microradiography and scanning electron microscopy (SEM) indicates their potential value in clarifying GLGs in the teeth of odontocetes.

Microradiography provides a non-destructive means of determining mineral density differences within hard tissues. It is particularly useful in resolving GLGs since GLGs consist of alternating poorly mineralized and more highly mineralized layers. It involves the use of very concentrated, low-voltage x-rays to expose a high resolution photographic plate, which increases sensitivity over standard x-rays, and gives sharply defined images. This permits the detection of local variation in mineral content in the tooth sections, since the x-rays are absorbed chiefly by the calcium and phosphate in the tooth (Trautz, 1967). Areas of greater mineral density are radiopaque and appear as light zones. Radiolucent or dark zones are the poorly mineralized areas that allow more x-rays to expose the plate.

An advantage of microradiography is that mineral density can be compared to optical density on the same thin section. This technique has been used by Sergeant (1962) and Nielsen (1972) to study odontocete teeth. Sergeant mentions that radiography confirmed his hypothesis that the opaque zones of teeth of *Globicephala melaena* were the better calcified dentine while the translucent zones were poorly calcified. In the teeth of *Phocoena phocoena*, Nielsen found that the radiopaque layers are equivalent to the light layers on thin sections when viewed with transmitted light. Because this result is contrary to Sergeant's (1962) findings, Nielsen cautions that optical density may not be dependent on mineral density.

A less ambiguous method of resolving GLGs may be by the removal of superficial calcium from a half-section of tooth, a procedure referred to as etching. The mineral is dissolved in an acid, usually formic, nitric, or hydrochloric, or removed by a chelating agent such as EDTA (see Boyde and Jones, 1974). After drying, the surface of the section has a topography of alternating ridges and grooves, each pair of which corresponds to a GLG, that results from the greater collapse of dentinal tissue in those layers which were initially hypercalcified.

Although etching seems to be a good technique for enhancing GLGs in sperm whale teeth (Bow and Purday, 1966), it has not frequently been applied to small odontocetes, probably because of difficulty in counting individual ridges and grooves. One method to facilitate counting is by use of the SEM. The advantage of the SEM is that it produces a three dimensional image of the surface of the tooth, allowing for more accurate interpretation of the GLGs.

The purpose of this study is to compare the techniques of transmitted light microscopy, microradiography and SEM for examination of *Tursiops* teeth for the clear resolution of GLGs, identification of accessory layers, and correlation of mineral density with optical density for the layers.

METHODS

Two teeth were taken from each of 15 *Tursiops truncatus* females which had stranded on the east coast of the United States, and which are in the collection of the National Museum of Natural History. Generally the teeth were removed directly from the skulls, most of which had been boiled clean before addition to the collection. When possible, central mandibular teeth were extracted. If the teeth had already been removed from the jaws, large relatively straight teeth were chosen.

All teeth were sectioned with a *Buehler Isomet* 11-1180 low speed saw. Longitudinal half-sections were cut by gluing the tooth on a microscope slide with a cellulose nitrate base adhesive and cutting medially. For thin sections, the cut surface of one half-section was glued down on a slide and all but 150 μm cut off, leaving the thin section adhering to the slide. Sections thicker than 150 μm were sanded down using 320 and 400 grit sandpaper. To prepare thick cross sections the tooth was placed in a clamp-like chuck accessory of the saw and cut in the zone of most recent growth as determined from the longitudinal thin section. Another cut was made farther down the tooth to make the sections about 0.25 cm thick for use in the SEM.

Preparation for microradiography involved removal of the longitudinal thin sections from the slide and then cleaning it in an ultrasonic cleaner to remove loose surface particles. One section from a tooth of each animal was microradiographed, following the method of Ortner and Yong (1975), for one and one-half hours at 11 kv. GLGs were counted from the microradiograph using a dissecting microscope.

The cross sections prepared for SEM were soaked in 5% formic acid for three hours, rinsed in water, then sonically cleaned. Each section was air dried, mounted on an SEM stub, plated with gold-palladium, and viewed with a *Cambridge Stereoscan* Mk IIA or S4-10 or AMR 1000A SEM. Micrographs were taken at a 45° tilt-angle under low magnification (15–21X) at 10 kv for large sections and 20 kv for smaller sections, including at least one-half of the surface of the tooth from the center to the periphery. Details were viewed under higher magnification at 20 kv.

RESULTS

GLGs

GLGs are the most prominent layered components within the tooth (see workshop glossary for definitions), within which there are finer layers. Using light microscopy with undecalcified thin sections, each GLG is composed of a translucent and an opaque layer (Fig. 1). In etched sections, each GLG consists of a ridge and an adjacent groove (Fig. 2). In microradiographs, each GLG consists of one radiopaque and one radiolucent layer, indicating that each GLG comprises one hypermineralized layer and one hypomineralized layer (Fig. 3). Cross counts of GLGs using the three methods gave the same whole-year counts for most of the specimens. Discrepancies occurred in some cases where the microradiograph resolved the beginning of a new layer, resulting in a slightly higher count (Table 1), and where it made visible last-formed layers in older animals in which the pulp cavity had been occluded (Figs. 1, 2, and 3). In the latter case, the additional GLGs followed the periodicity and intensity of the preceding GLGs.

Figs. 1–3. Comparison of GLGs in the same tooth by each of the techniques used.

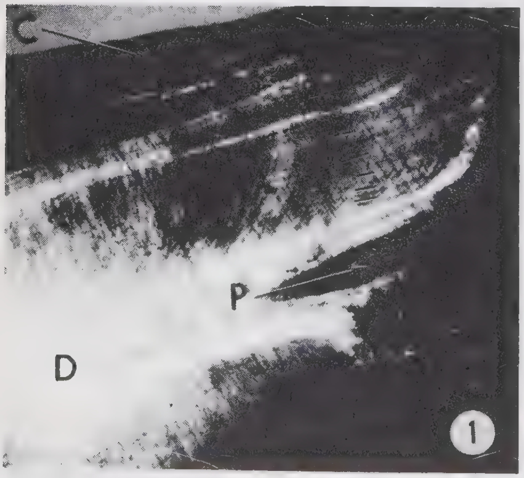

Fig. 1. Ground longitudinal section (150 μm) under polarized transmitted light. GLGs visible only on the sides of the tooth and near the base close to the pulp cavity. Bars demarcate GLGs. Original magnification: ×17. P – pulp cavity, C – cement, D – dentine.

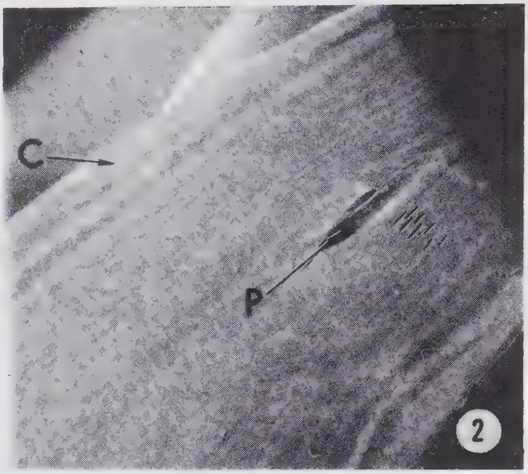

Fig. 2. Scanning electron micrograph of etched longitudinal half-section. GLGs more clearly resolved than in thin section. Original mag.: ×15.

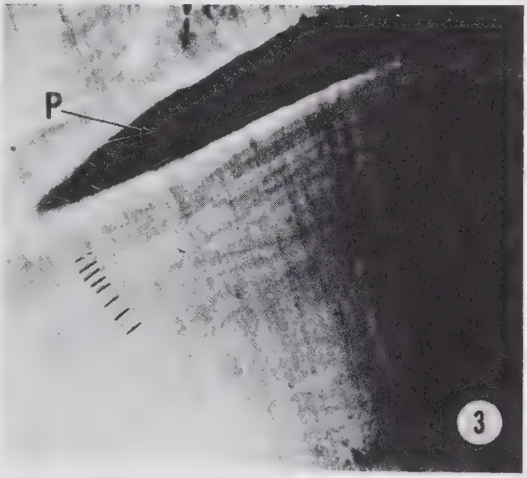

Fig. 3. Microradiograph of ground thin section. More GLGs appear surrounding the pulp cavity than are resolved either by light microscopy or SEM. Original mag.: ×25.

Table 1

Examples of discrepancies in dentinal GLG counts in teeth of *Tursiops* compared by method of examination. Light microscopy counts were made using transmitted polarized light. TL – total length of the animal

		Number of GLGs counted		
USNM No.	TL (cm)	Light microscopy	SEM	Micro-radiography
504590	155	1	1	1¼
504583	185	3	3	3¼
395670	–	12	12½	12½
504559*	252	14	14	18

*Pulp cavity occluded.

Incremental growth layers

Incremental growth layers are layers which occur parallel to the formative surface of the dentine (see workshop glossary) and compose GLGs. In cross sections of teeth, incremental growth layers are arranged concentrically around the pulp cavity (Figs. 4 and 7). They are most prominent in SEM micrographs where they appear as fine ridges and grooves within the ridges and grooves of the GLGs. In microradiographs and thin sections viewed with light microscopy, incremental growth layers appear as adjacent fine radiolucent and radiopaque layers or translucent and opaque layers, respectively, but are not as clear as in the SEM micrographs. The incremental growth layers averaged 10 to 13 per GLG and 2.0 μm to 3.5 μm in width measured from SEM micrographs, with those in the most recently formed GLGs sometimes smaller than those in the first formed GLGs. Although they were in all of the teeth, they were often not apparent in old animals in the first-formed GLGs nor in the compressed, last-formed GLGs. In sections which showed incremental growth layers in the last-formed GLG, there was a constant number in the teeth of animals that died during the same time of year.

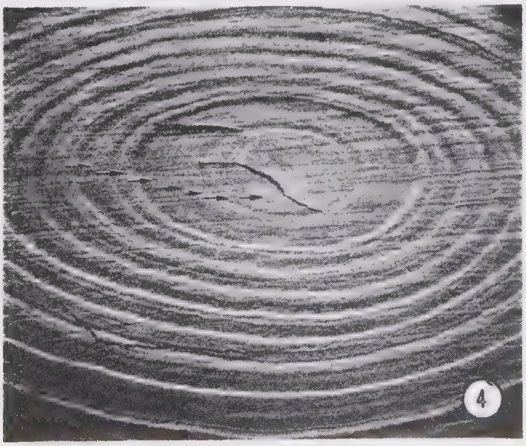

Fig. 4. SEM of etched cross section showing the alternating ridges and grooves. Also faintly visible are some incremental growth layers which compose the GLGs. Arrows indicate GLGs. Original mag.: ×50.

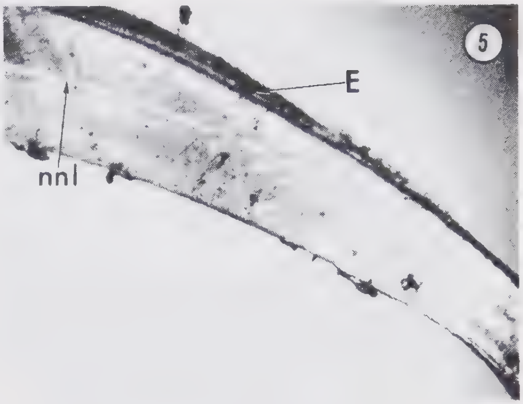

Fig. 5. Ground thin section from the tooth of a young animal viewed under polarized transmitted light. The many accessory layers prevent accurate distinction of the beginning of a new GLG. The neonatal line appears translucent. Original mag.: ×30. E – enamel, nnl – neonatal line.

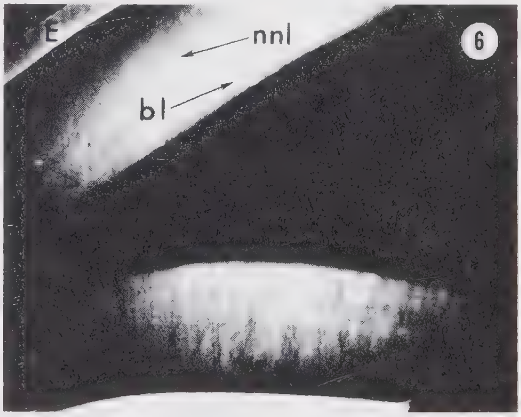

Fig. 6. Microradiograph of the ground thin section in Fig. 5. One radiolucent line stands out and is considered the GLG boundary layer. Original mag.: ×30. bl – boundary layer.

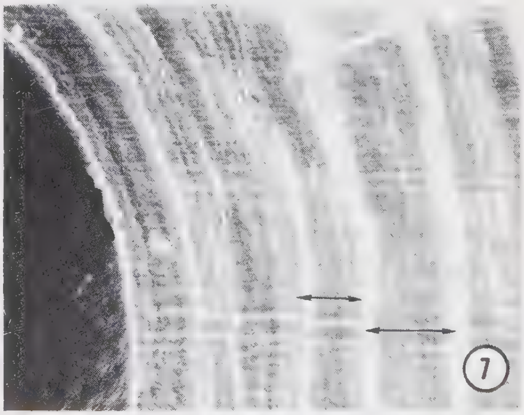

Fig. 7. SEM micrograph of an etched cross-section showing the incremental layers, arranged concentrically around the pulp cavity, which compose the GLGs. The lines running from left to right are saw marks; dentinal tubules are not visible. The arrows denote GLGs. Original mag.: ×180.

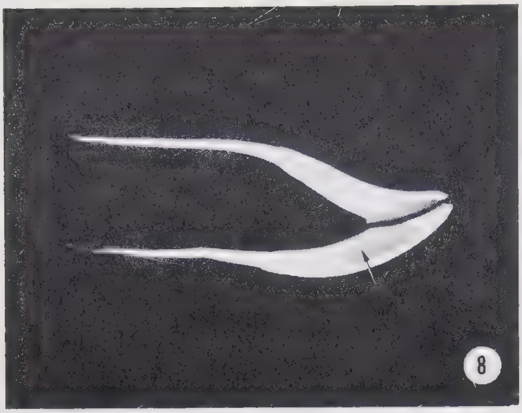

Fig. 8. Microradiograph of ground thin section. The enamel is strongly radiopaque (light), the neonatal line radiolucent. Slight differences in thickness of the section prevented the x-rays from exposing the plate at the root end of the tooth, so it appears highly mineralized (radiopaque). The arrow indicates the neonatal line. Original mag.: ×7.

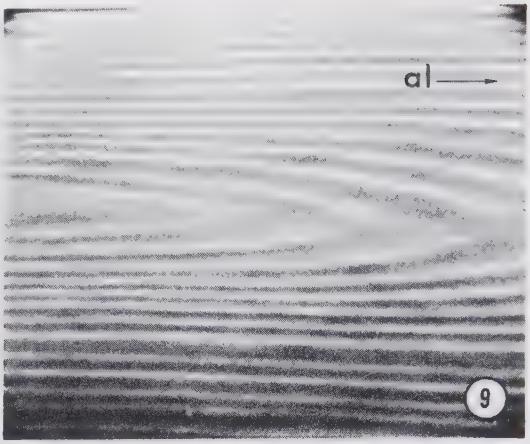

Fig. 9. SEM micrograph showing an accessory layer as an additional ridge between two GLG ridges.

Accessory layers

Sometimes an incremental layer appears particularly prominent within the GLG because it is relatively more hypo- or hypermineralized than the GLG layer in which it is located (Fig. 9). For purposes of this study, these prominent layers are referred to as accessory layers, defined as irregularly occurring, nonrhythmic layers that disrupt the expected mineralization pattern within a GLG and complicate the problem of counting GLGs. They seem to occupy the same relative position in GLGs in the teeth of a given individual, but vary in number and position among teeth of various specimens. Accessory layers occur most commonly near boundaries of GLG layers.

Comparison of techniques for counting GLGs

Scanning electron micrographs of etched sections is the easiest method by which to count GLGs, because the contrast in topographic relief between the layers of a GLG is generally great enough to easily distinguish adjacent GLGs (Fig. 4). Although incremental layers and accessory layers are apparent using SEM, their effect in confusing the counting of GLGs is diminished by etching. In microradiographs, the first-formed GLGs are not as clearly delineated, because the contrast between adjacent layers of the GLG is less than in etched sections. In undecalcified thin sections examined with light microscopy, the accessory layers were sometimes so conspicuous near the boundary layer of GLGs that divisions between GLGs were obscured. This problem occurred most often within the first four or five GLGs. When the boundaries of the GLGs were not definable, the number of GLGs could only be estimated.

Correlation between optical and mineral density

Optical density corresponds to mineral density for each layer of the GLG when comparing the three methods (Table 2). Sections viewed with transmitted light show the neonatal line as translucent with the prenatal zone and the immediately postnatal incremental layer of the first GLG appearing opaque, and the second layer of the GLG appearing translucent. In etched sections, the neonatal line appears as a ridge, and the prenatal and immediately postnatal incremental layer are grooves. In the microradiographs, the neonatal line is radiolucent (relatively hypomineralized), the prenatal and postnatal incremental layers are radiopaque (relatively hypermineralized), with the second incremental layer of the GLG radiolucent. This cyclic deposition of mineral, i.e. adjacent hypermineralized and hypomineralized layers, continues throughout the postnatal dentine.

Table 2
Correlation of GLG components with relative mineral density in the teeth of 15 specimens of *Tursiops* using transmitted light microscopy, SEM, and microradiography

Method of examination			
Transmitted light	Microradiography	SEM	Relative mineral density
opaque	radiopaque	groove	greater
translucent	radiolucent	ridge	less

DISCUSSION

GLGs

Each of the preparations should permit adequate age estimates to the nearest whole GLG, but microradiography seems to be the best of the three techniques for accurately identifying the nature, i.e. mineral density, and extent of growth of the newly forming GLG in teeth which were still accumulating dentine when the animals died. This information, collected over at least a year for a species, will show the cycle of mineralization, helping to explain the mechanisms influencing mineralization and its relationship to life history attributes of the animals. Previous work, e.g. on *Tursiops truncatus* (Sergeant, 1959), *Globicephala melaena* (Sergeant, 1962), *Hyperoodon ampullatus* (Christensen, 1973), *Delphinapterus leucas* (Sergeant, 1973), and *Berardius bairdii* (Kasuya, 1977), has shown the consistency of the stainability or optical density of the last GLG component with the season of death for each species.

In some cases, more GLGs may be deposited, in terms of mineralization cycles, than may be determined using conventional light microscopy. Because of its sensitivity to differential mineral density, microradiography may be used to detect these GLGs and extend the maximum GLG count.

Incremental growth layers

Early work in dental histology demonstrated the existence of incremental lines in dentine that express the constant rhythmic changes in the degree of mineralization of the matrix (Schour and Steadman, 1935; Schour and Hoffman, 1939a; Schour and Massler, 1940). According to Schour and Hoffman (1939a), two adjacent lines, one more and one less mineralized, measured 16 μm in all species examined. These lines were later interpreted as incremental lines of von Ebner. More recently, smaller incremental lines (von Ebner lines), e.g. 5 μm, have been described that represent daily increments of growth of the tooth (Krauss and Jordan, 1965; Miani and Miani, 1972; Newman and Poole, 1974; and Yilmaz, Newman, and Poole, 1977). However, neither incremental growth of teeth on other than a daily rhythm nor the annual mineralization pattern of mammal teeth have been well demonstrated.

Sub-annual incremental layers, where GLGs in at least *Tursiops* teeth are considered to be annual (see Sergeant, 1959; Klevezal' and Kleinenberg, 1967; Sergeant *et al*, 1973; this workshop–known-age dolphins), have been described in some marine mammals. Kasuya (1977) found the 'long cycles' (GLGs) in *Berardius* teeth to contain many (11.0–13.4) 'short cycles', and Kasuya and Nishiwaki (1978) found that coarse layers (GLGs) in *Dugong* tusks contain 10 to 15 fine growth layers (see also Scheffer, 1970). They interpreted the fine growth layers or short cycles as representing the lunar cycle or an endogenous rhythm of about one month manifested in the growth of the tooth. Myrick (this volume) noted incremental layers (his accessory lines) of the same periodicity in the teeth of different species of dolphin, as well as von Ebner lines which are interpreted as representing a daily growth pattern. The rhythmicity and periodicity of the incremental lines or layers, i.e. 10 to 13 per GLG, in this study, also suggests the incremental layers in the North Atlantic Ocean *Tursiops* to be incremental growth of the tooth similar to that described by Kasuya (1977), Kasuya and Nishiwaki (1978) and Myrick (this volume). In this case, the incremental layers appear to be the result of a finer mineralization pattern within the more gross annual mineralization cycle of the GLGs. This is evident in the three-dimensional pattern of the incremental layers in etched sections, where calcium has been removed, and in microradiographs.

Accessory layers

If the mineralization cycles, both annual and sub-annual, seen in dolphin teeth are the result of extrinsic environmental factors, then irregular changes in the expected deposition pattern may be a visible manifestation of a change in environmental parameters. Similarly, if mineralization is intrinsically controlled, appropriate changes within the animal's system should appear in an actively growing tooth. Accessory layers may be a result of either of these types of fluctuations. If so, they may be useful in distinguishing stocks of animals, and careful notation of these changes may aid in explaining mechanisms responsible for the mineralization patterns seen in dolphin teeth; therefore, it is important to distinguish accessory layers as such. But, in regards to a practical application of odontocete teeth for age determination, a method is needed that permits clear resolution of individual GLGs without the sometimes overwhelming interference of accessory layers. Of the three methods in this study, SEM best serves this purpose.

Correlation between optical and mineral density

The determination of the mineral density of each layer of a GLG, especially the last-formed layer, may be important for resolving the basis of formation of GLGs in odontocete teeth. However, there has been disagreement about the interpretation of optical density and mineral density in some of the species examined (Sergeant, 1962; Klevezal' and Kleinenberg, 1976; Nielsen, 1972; and Kasuya, 1976). In response to these discrepancies, Nielsen (1972; this volume) feels that no species-wide generalization can be made to correlate optical to mineral density.

In this study, the correlation of mineral density to optical density in the teeth of *Tursiops* agrees with Sergeant's (1962) results with *G. melaena.* In agreement with many previous studies (*Stenella coeruleoalba,* Nishiwaki and Yagi, 1953; *T. truncatus,* Sergeant, 1959; *G. melaena,* Sergeant, 1962; *B. bairdii,* Kasuya, 1977; and *Phocoena phocoena,* Gaskin and Blair, 1977) the neonatal line is translucent (or unstainable) and the immediately postnatal layer is opaque (transmitted light). Although the event causing the formation of the neonatal line does not occur again, the neonatal line is hypomineralized (Irving and Weinmann, 1948) and is generally easily identifiable. Therefore, it can be used as a landmark for identification of mineral densities of the following layers. In other words, if the neonatal line appears translucent, and we know it to be hypomineralized by microradiography, then each translucent layer within subsequent GLGs should be hypomineralized. This is the case in all of the *Tursiops* teeth examined.

Evaluation of techniques

Of the three techniques, SEM is the easiest method by which to count GLGs. While the method is procedurally more complicated than preparation of thin sections, the results justify the slight additional preparation time, especially for a large number of specimens. Microradiography, valuable as a source for information on mineral density, requires exceptional precision in thickness of sections and timing of the x-ray to achieve worthwhile results and would be too demanding for age determination of a large number of specimens. The conventional method of light microscopy, although less complicated in terms of tooth preparation, seems to be least reliable for accurate counting of GLGs.

Although each of the methods permits adequate estimates of GLGs for age determination, additional information about the deposition and mineralization of dentine is available from microradiography and SEM. Such information helps to better define GLGs, as well as to ascertain what processes influence layering in odontocete teeth.

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I am grateful to D. Ortner and D. Yong, Department of Anthropology, U.S. National Museum of Natural History (NMNH), Smithsonian Institution, for the suggestion and use of their microradiograph. C. Potter and G. Morgan, NMNH, critically reviewed the manuscript; J. Bittner, NMNH, helped in preparation of figures. M. Jacque Mann, SEM Lab, NMNH, prepared most of the SEM micrographs. A. Myrick, National Marine Fisheries Service, encouraged me during the early stages of this research. I am especially indebted to J.G. Mead, NMNH, whose advice and support enabled me to complete this work.

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A METHOD FOR AGE DETERMINATION OF DOLPHINS

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The use of growth layers in teeth as an indicator of age in odnotocetes and pinnipeds was suggested by Laws (1954) and since then the method has been used extensively in both marine and non-marine mammals. Dentinal growth layers are groups (growth layer groups) of repetitive alternating bands which in cross-section are similar to growth rings in trees. The most commonly used methods for counting growth layer groups (GLGs) are by undecalcified longitudinal thin sections (150 um) or decalcified and stained thin sections (10-30 um). In longitudinal sections viewed with light microscopy, GLGs appear as opaque and translucent cones nestled one inside another, with the oldest dentine lying adjacent to the enamel, and the newest layer bordering the pulp cavity.

Each GLG consists of two layers differentiated by optical or mineral densities, and, in at least dolphins (family Delphinidae), evidence from captive and marked animals has shown that one GLG is deposited each year. During one part of this annual cycle a layer of dentine is relatively hypomineralized; during the remainder of the cycle the dentine is relatively hypermineralized. Conventional methods of counting GLGs have used this mineral pattern to differentiate GLGs by corresponding differences in optical densities visible in thin sections or by differential stainability of the layers.

Although most of the methods currently employed in defining and counting GLGs yield adequate results, the clarity of layering is often poor with repeated counts on sections of teeth giving different results because of fine "accessory layers" interfer with boundaries GLGs. An alternative method for resolving GLGs is by etching the tooth, i.e. removing superficial calcium, which produces a pattern of alternating ridges and grooves, which are easily seen in large sperm whale teeth but the small size of some dolphin teeth (e.g. Stenella sp., about 0.3 cm diameter, and Turiops, about 0.6 cm diameter) prohibits the use of the method with more conventional microscopic techniques. The use of SEM on etched sections of small dolphin teeth greatly facilitates the counting of GLGs over these conventional methods.

Cross-sections (0.25 cm) or logitudinal half-sections of teeth were cut on a Buehler Isomet low speed saw. Each section was etched in 5% formic acid for three hours, rinsed in water, cleaned in an ultrasonic cleaner in acetone, then dipped in 70% ehtanol. Each prepared section was then air dried, mounted on an SEM stub, coated with gold-palladium, and viewed with a Cambridge Stereoscan MKIIA or S4-10 SEM. Micrographs were taken at a 45-55 tilt angle.

Micrographs show the clear resolution of GLGs as ridges and grooves (figure 1 and 2), in many cases without the interferences of accessory layers. In addition, a finer pattern of layering can be seen, at least in young animals where the pulp is not yet accluded, which seems to indicate a rhythmic pattern of dentine deposition as incremental lines within each GLG (figure 3). This method seems to offer the clearest way to resolve and coung GLGs in the teeth of small dolphins and is useful to identify additional structures in the dentine.

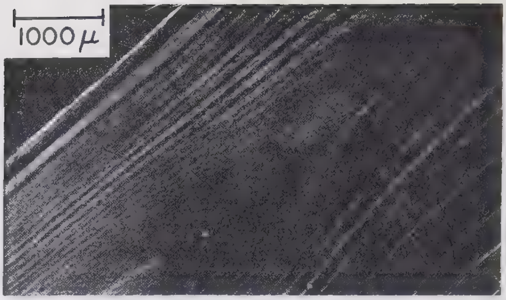

Figure 1: An etch longitudinal section of tooth from an old bottlenose dolphin, *Tursiops truncatus*, with 18 GLGs, where each GLG consists of one ridge and one groove. The occluded pulp cavity indicates that this is only a minimum age.

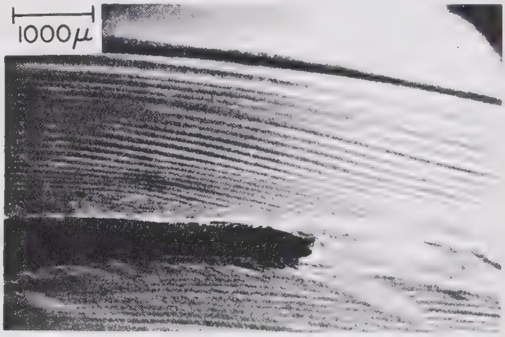

Figure 2: Longitudinal section of a tooth from *Tursiops* with at least 20 GLGs and an open pulp cavity. Cementum, which surrounds the dentine, is visible at the bottom of the picture.

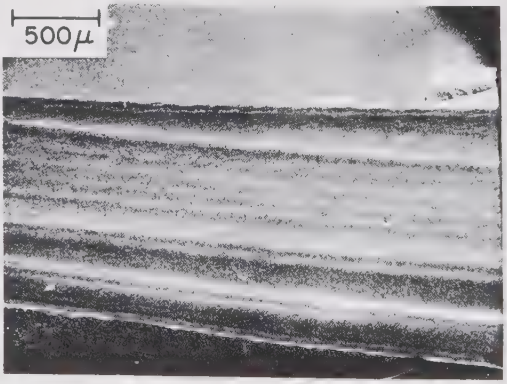

Figure 3: Incremental lines which compose the two GLGs in this tooth are visible in this section from a young *Tursiops*.

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Quarterly

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AN IMMUNOLOGICAL APPROACH FOR CTX

by Y. Hokama[1], L.H. Kimura[1], K. Shiraki[1],
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INTRODUCTION

The application of immunological techniques for the detection of low molecular weight, nonimmunogenic compounds has increased markedly in the past decade. The ability to conjugate these haptenic small molecules covalently to appropriate immunogenic carriers via their functional groups has led to the production of specific antibodies to the haptenic molecules following administration into appropriate animals. Primary functional groups or moieties amenable to conjugation, provided they are accessible to chemical coupling, include amino, hydroxyl, and carboxyl groups. Some common methods for coupling include carbodiimide, nucleophilic substitution, diazo and azide coupling. In some cases, for example with lipid antigens, noncovalent complexes have been utilized using methylated bovine serum albumin as the carrier (Butler et al., 1973; Becher, 1976).

The production of a specific antibody to the low molecular weight compounds can then be utilized for the development of sensitive and specific immunological procedures such as radioimmunoassay (RIA) and enzyme-linked immunoabsorbent assay (ELISA) for detection of minute amounts of antigens or antibodies. In addition, the antibodies are useful in examining other areas of study such as tissue distribution, synthesis and in some cases the structure and function of the haptenic molecule.

The application of the sensitive immunological methods for the detection of marine toxins, such as saxitoxin, ciguatoxin, and tetradotoxin, merits strong consideration in light of the minute amounts of these toxins in the natural environment. The minute amount in tissues has constituted serious hazards to the consumer and has created anxiety within the fishing and shellfish industries.

This study discusses the immunological approaches for the development of a radioimmunoassay procedure for the detection of ciguatoxin (Hokama et al., 1977). The methodology presented is applicable for the development of immunological procedures for the other low molecular weight marine toxins such as saxitoxin, tetradotoxin, and *Gymnodinium breve* toxins. In addition, for correlative analysis, the guinea pig atrium procedure (Miyahara et al., 1979) for quantitation of ciguatoxin and maitotoxin from crude extracts of fishes is also included in this study. Comparison of the RIA procedure with the mouse M.U. test is also presented in this study.

METHODS FOR CIGUATOXIN ANALYSIS

The development of the RIA procedure for the direct detection of ciguatoxin (CTX) from fish tissues has been reported previously (Hokama et al., 1977).

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Purified ciguatoxin (Scheuer et al., 1967) isolated from livers of toxic eels was conjugated by the carbodiimide procedure (Oliver et al., 1968) to human serum albumin (HSA). The latter is the carrier for the lipid hapten-ciguatoxin. Precipitation of the ciguatoxin-HSA (CTX-HSA) with cold acetone indicated that CTX was in the precipitate (CTX-HSA) and not in the acetone phase. This suggested that most if not all CTX was bound to HSA.

The antibody to CTX-HSA was raised in sheep given three weekly subcutaneous injections of a CTX-HSA-Freunds complete adjuvant mixture (1:1). A total of 500 μg of CTX and 50 mg of HSA (CTX-HSA) was administered to the sheep in a period of 7 weeks. The sheep was bled 10 days after the last injection and the serum removed and stored in 30 ml aliquots at -20°C.

The details of the determination for the presence of anti-CTX-HSA by immunoelectrophoresis and mouse studies and for the development of the RIA procedure have been described (Hokama et al., 1977). In brief, the RIA method consists of the following steps: (1) sample tissues from the dorsal and ventral muscles, tails, or gonads of the fish; (2) dehydrate samples in oven at 70°C for 1 hour; (3) after cooling, weigh 15-mg samples; (4) rehydrate with buffered saline; and then remove buffer; (5) add 0.2 ml of ^{125}I-labelled sheep anti-CTX-HSA (sp. act., 1.03 mCi/mg protein) containing 50,000 cpm/0.1 ml; (6) shake for 3 hours at room temperature; (7) add 3.0 ml buffered saline; (8) aspirate buffer thoroughly; and (9) count the sample in gamma-counter. After background correction, the cpm/tube is divided by 15 mg to give cpm/g tissue. Samples are determined in triplicates, or duplicates in some instances. Toxic and nontoxic fish tissue samples are examined with each set of unknown determinations.

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The present study includes examination by the RIA procedure of fishes recovered from clinically diagnosed ciguatera poisoning cases and nontoxic fishes from commercial sources. The toxic fishes were obtained through the courtesy of the Hawaii State Department of Health. The nontoxic fish samples were obtained from various commercial and noncommercial sources. Reef fishes from Tahiti were obtained through the courtesy of Dr. Bagnis of the Institut de Recherches Medicales Louis Malarde.

A correlative study of the RIA procedure and the *in vitro* guinea pig atrium assay was carried out for several samples of toxic and nontoxic fish tissues. The details of the guinea pig atrium analysis were reported recently by Miyahara et al. (1979). The crude extracts of the fish tissues were prepared according to a previously described procedure (Yasumoto et al., 1977). A 20-g tissue is homogenized and extracted with 200 ml hot methanol. The residue is removed by filtration and the methanol phase concentrated to 10 percent of the original volume. The concentrated solution is diluted with distilled water (5 volumes) and the lipid solutes extracted with diethyl ether. The ether is evaporated and the crude lipid residue dissolved in minimal methanol and stored at -20°C until ready for study. Assay for the mouse toxicity procedure has been described previously (Yasumoto et al., 1971).

Based on the examination of fishes from human ciguatera poisoning and previous results obtained by RIA (Hokama et al., 1977) the following arbitrary criterion has been established relative to the cpm/gm tissue values.

Cpm/gm Tissue	Toxicity Index
< 350,000	Negative
350,001 to 399,999	Borderline
> 400,000	Toxic

The diagnosis of ciguatera poisoning of patients following consumption of suspected toxic fishes is based on the clinical symptoms described previously (Okihiro et al., 1965; Bagnis, 1968).

RESULTS

RIA Examination of Fish Samples. The results of the examination of individual cases of fish samples recovered from clinically diagnosed ciguatera

Table 1. RIA Examination of Fish Samples From Clinically Documented Ciguatera Poisoning

No. of Samples	Fish Species	Common/Hawaiian Name	RIA Results CPM/GM Tissue	Remarks
3	*Scarus* sp.	Parrotfish/uhu	463,039	Toxic
	Scarus sp.	Parrotfish/uhu	524,106	Toxic
	Scarus sp.	Parrotfish/uhu	421,064	Toxic
1	*Elagatis bipinnulatus*	Rainbow runner/kamanu	463,636	Toxic
6	*Seriola dumerilii*	Amberjack/kahala	415,870	Toxic
	Seriola dumerilii	Amberjack/kahala	549,534	Toxic
	Seriola dumerilii	Amberjack/kahala	412,600	Toxic
	Seriola dumerilii	Amberjack/kahala	447,045	Toxic
	Seriola dumerilii	Amberjack/kahala	436,778	Toxic
	Seriola dumerilii	Amberjack/kahala	296,667	Toxicity not detected by RIA
13	*Caranx* or *Carangoides* sp.	Jack/ulua	414,489	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	420,667	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	492,634	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	505,779	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	497,406	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	400,867	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	711,346	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	448,936	Toxic
	Caranx or *Carangoides* sp.	Jack/ulua	351,400	Borderline
	Caranx or *Carangoides* sp.	Jack/ulua	387,553	Borderline
	Caranx or *Carangoides* sp.	Jack/ulua	362,920	Borderline
	Caranx or *Carangoides* sp.	Jack/ulua	370,597	Borderline
	Caranx or *Carangoides* sp.	Jack/ulua	300,300	Toxicity not detected by RIA
2	*Mugil cephalus*	Mullet/ama'ama	449,967	Toxic (viscera sample)
	Mugil cephalus	Mullet/ama'ama	462,753	Toxic
1	*Aprion virescens*	Grey-snapper/uku	482,133	Toxic
1	*Monotoxis grandoculis*	Porgy/mu	660,556	Toxic
1	*Priacanthus cruentatus*	Red big eye/aweoweo	382,584	Borderline
1	*Lutjanus gibbus*	Paddle-tail snapper	442,000	Toxic
3	*Epinephelus mario*	Sea bass	479,339	Toxic
	Epinephelus mario	Sea bass	490,392	Toxic
	Epinephelus mario	Sea bass	375,189	Borderline

poisoning are indicated in Table 1. A variety of species has been implicated, including the following species: *Scarus* sp., parrotfish/uhu; *Elagatis bipinnulatus*, rainbow runner; *Seriola dumerilii*, amberjack/kahala; *Caranx* and *Carangoides*, sp., jack/ulua; *Mugil cephalus*, mullet/ama'ama; *Aprion virescens*, grey snapper/uku; *Monotoxis grandorulis*, mu; *Priacanthus*, sp., red big eye/aweoweo; *Lutjanus gibbus*, paddle-tail snapper; and *Epinephelus mario*, sea bass. Two samples, a *Seriola dumerilii* and a *Caranx* sp., gave RIA values in the nontoxic range. The mean ± 1 S.D. (434,654 ± 110,184) value for the 32 toxic samples is summarized in Table 2. This value is significantly ($p < 0.001$) different from the mean ± 1 S.D. (264,202 ± 44,291) value of the 91

Table 2. Summation of RIA Values for Fishes From Clinically Defined "Ciguatera Poisoning" Cases and Nontoxic Fishes

Fish	CPM/GM Tissue (Mean ± 1 S.D.)		
	Nontoxic	Toxic	p*
Several Species†	264,202 ± 44,291 (n = 91)	434,654 ± 110,184 (n = 32)	< 0.001

*p value based on two-tailed analysis.

†See Table 1 for the individual species listed for the toxic group; the nontoxic fishes in this category were sampled from the same species implicated in the "ciguatera poisoning" or the toxic group.

non-toxic samples of essentially the same species shown in Table 1.

Comparison of the RIA with the Mouse Toxicity, M.U. Figure 1 summarizes a comparative study of the RIA with the mouse toxicity of reef fish tissues obtained from Tahiti. The incidence of ciguatera poisoning is high in French Polynesia in contrast to other areas of the Pacific. The coefficient of correlation, r, is moderate between RIA:M.U. The r values are summarized in Table 3. The RIA:Mongoose r value from a previous report (Hokama et al., 1977) is also shown in Table 3.

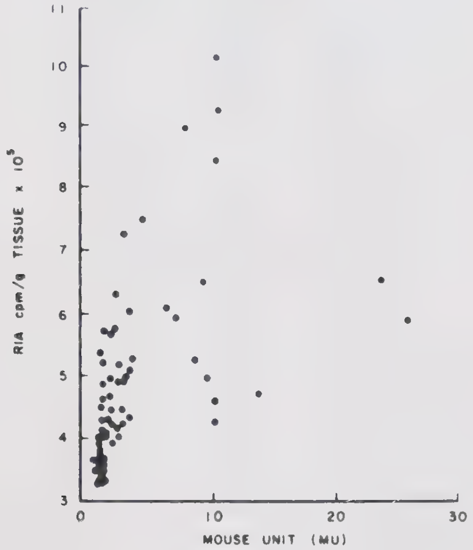

Figure 1. Comparison of RIA procedure for ciguatoxin detection and the mouse toxicity based on M.U.; each circle represents a sample. (RIA values are average of triplicate samples.)

Comparison of RIA with Guinea Pig Atrium Assay. This correlative study between the RIA and inotropic effect of ciguatoxin on guinea pig atrium is presented in Figure 2 with the r value shown in Table 3 (r = 0.88). Although the sample number is small, a significantly good correlation is shown between the RIA and guinea pig atrium assay. The latter assay appears to be a valuable method for ciguatoxin studies in correlation with the RIA and other biological procedures.

Table 3. Summation of the Comparison of the RIA Procedure with the Other Biological Methods for the Evaluation of Ciguatoxin

No. of Samples	System	Coefficient of Correlation (r)	Reference
66	RIA:M.U. (mouse)	0.56	Hokama et al., 1980
66	RIA:Mongoose	0.56	Hokama et al., 1977
13	RIA:Guinea pig atrium	0.88	Hokama et al., 1980

M.U. = Total weight in gm of mice killed within 48 hours by a 1 ml extract from 20 gm of fish tissue (Yasumoto et al., 1971).

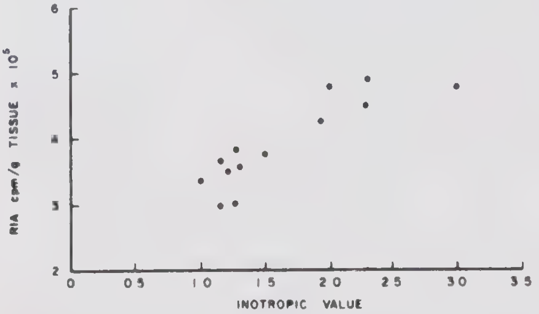

Figure 2. Comparison of the RIA procedure for ciguatoxin detection and the inotropic effect on guinea pig atrium. The inotropic values indicated are obtained by dividing the increase in amplitude (inotropic effect) by the base line contraction.

DISCUSSION

A general approach for the use of immunological procedures for application to small molecules is presented elsewhere (Hokama et al., 1980). The significant factors include: (1) the importance of coupling of the low molecular weight compounds to appropriate antigenic carriers, that is, presentation in positions of accessibility, without gross changes in the haptenic molecule; and (2) selection or choice of the antigenic carrier. Of equal importance is the choice of animal for the production of antibody and the mode of administration of the hapten-carrier conjugate. The analysis and development of the immunological methods for the antibody raised will depend on the levels of the antibody and the haptenic molecule to be examined (Landsteiner, 1945; Rose and Friedman, 1976).

Essentially following the general procedures presented elsewhere (Hokama et al., 1980), development of an immunological procedure for the detection of ciguatoxin (a lipid hapten) has been initiated earlier (Hokama et al., 1977). This study presents further evaluations of the RIA procedure by examining various species of fishes including those specimens implicated in ciguatera poisoning.

The comparative examination of fish samples from Tahiti with the RIA and mouse (M.U.) procedure gave an r value which appeared to be similar (Table 3) to that demonstrated earlier for RIA and mongoose. The lack of a better correlation may be due to the highly sensitive nature of the RIA test as discussed previously (Hokama et al., 1977). The capability and limitations of the biological procedures have been discussed earlier by other investigators (Banner et al., 1960; Banner et al.,1961; Kosaki et al., 1968).

The present state of the RIA procedure is significantly sufficient to distinguish toxic from nontoxic fishes. Furthermore, the test appears to be helpful for the examination of various species of fishes from different geographical areas for the evaluation of the presence or absence of toxic fishes. For example, coral reef fishes from Tahiti tended to have a higher incidence of toxic levels and cpm/gm tissue than similar species caught in Hawaii. (Compare data on fishes from Tahiti in Figure 1 with data on fishes in Hawaii in Table 2.) Thus, in its present state the RIA procedure can be utilized for the exploration of the levels of toxicity and distribution among various fish species in different geographic areas, especially where ciguatera poisoning is endemic. This would aid in the development of the fishing industry.

The limitations of the RIA procedure for wide-scale use at present include: (1) restrictions on the number of sampling per day by a technologist; and (2) a minimum of approximately 6 hours required for the completion of the test. Other difficulties include: (1) sampling error, that is, the uncertainty of toxin distribution or localization in various parts of the tissue; (2) a tendency for false positive reactions due to nonspecific binding; and (3) reproducibility due to the fact that tissues are utilized, and even within close proximity "hot spots" of ciguatoxin may vary.

Efforts are currently being directed towards decreasing the test time, devising an ELISA procedure using homogenous crude lipid extracts from large tissue areas, minimizing the cost of the test, and increasing specificity by attempting to isolate and concentrate the specific antibody involved. In addition, the development of immunofluorescent procedures would be helpful in assessing the presence of ciguatoxin in *Gambierdiscus toxicus* (Figure 3) (Yasumoto et al., 1977).

The need for a specific, sensitive, and simplified procedure for the detection of ciguatoxin is evident in a recent report (Morris, 1980) from the Center for Disease Control, Atlanta, Georgia. Ciguatera poisoning has been reported as the leading cause of poisoning from marine foods in the United States, surprisingly even more so than paralytic shellfish poisoning (Morris, 1980).

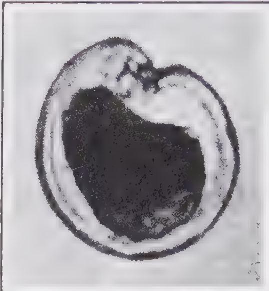

Figure 3. *Gambierdiscus toxicus* (400X)

SUMMARY

The steps involved in the utilization of immunological procedures to study small molecules including marine toxins are as follows: (1) conjugation of the small molecule to appropriate antigenic carriers; (2) immunization of animals for the production of antibodies; and (3) development of an immunological method for analysis of the small molecule. The development of the radioimmunoassay for ciguatoxin was carried out accordingly. The RIA procedure for detection of ciguatoxin showed moderate correlation with the mouse M.U. (r = 0.56) test. These results were similar to that reported for the RIA and mongoose (r = 0.56) test. A good correlation of the RIA with the *in vitro* guinea pig atrium assay was demonstrated (r = 0.88). Examination of nontoxic fishes and fishes recovered from patients with clinically defined ciguatera poisoning with the RIA procedure demonstrated that the test clearly differentiated toxic from nontoxic samples. It is suggested that the RIA test in its present state is useful for the assessment of toxic from nontoxic fish tissue in a variety of fish species from various endemic areas. Currently work is being carried out to develop a simpler enzyme-linked immunoabsorbent assay with increased specificity.

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PRELIMINARY RESULTS OF STUDIES ON FECUNDITY OF THE SPINY LOBSTER, PANULIRUS MARGINATUS, IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Part of an investigation of the marine resources of the Northwestern Hawaiian Islands includes studies on the biology of the spiny lobster, *Panulirus marginatus*. This paper deals with the fecundity of *P. marginatus* collected from Necker Island and Maro Reef during 1978-79. Estimates of fecundity were made on 34 egg-bearing females. The number of eggs carried generally increased in relation to an increase in carapace length (CL). The smallest female (56.7 mm CL) in the sample carried an estimated 129,000 eggs. The largest female (104.6 mm CL) was found to have an estimated 454,000 eggs.

Northwestern Hawaiian Islands
Panulirus marginatus
fecundity

INTRODUCTION

The spiny lobster, *Panulirus marginatus*, which is endemic to the Hawaiian Archípelago and Johnston Atoll (Brock, 1973), is of great importance in the sport and commercial fisheries in the major Hawaiian Islands. Trapping surveys in the Northwestern Hawaiian Islands (NWHI) indicate that this species is taken at depths greater than 28 m (10 fathoms) (see paper by Uchida et al., part I).

One of the biological parameters of interest in the management of the resources is fecundity. Fecundity of *P. marginatus* caught off Oahu was previously estimated by Morris (1968) and by McGinnis (1972). However, no estimates have been made for *P. marginatus* caught in the NWHI; therefore, a study was initiated to determine their fecundity and also to examine whether significant differences occured in fecundity among lobsters caught at different localities throughout the archipelago.

METHODS

The material used in this report was collected at Necker Island and Maro Reef during cruises of the NOAA ship Townsend Cromwell (TC-78-04 and TC-79-02) during October 20-27, 1978 and March 31-June 6, 1979. The lobsters were caught in the California two-chambered lobster pot (Uchida and Hida, 1977). The traps were baited and set in the late afternoon and picked up the next morning. Thirty-four egg-bearing or "berried" females were collected during these cruises.

The carapace length, defined as the distance along the mid-dorsal line from the transverse ridge between supraorbital spines to the posterior margin of the carapace, was measured to the nearest 0.1 mm. In the field, egg masses were collected by carefully stripping the setae of pleopods on which the egg masses were attached. The egg masses collected from each pleopod were then frozen separately for later examination in the laboratory.

In the laboratory, the egg masses from each pleopod were preserved in a solution of 4% formaldehyde and seawater and allowed to harden for about 30 days. Before processing the egg masses, they were blotted with paper towels for 15 minutes and weighed to the nearest 0.001 g. Total weight of the egg masses was derived by summing the weight of the egg mass on each pleopod. A sample of eggs weighing approximately 0.125 g was then taken from each pleopod to make up a sample of 1 g. All the eggs in this sample were counted. The total number of eggs carried was then calculated by simple proportion:

$$\frac{\text{Weight of sample}}{\text{No. of eggs in sample}} = \frac{\text{Total weight of eggs}}{\text{Total no. of eggs carried}} \qquad (1)$$

RESULTS

Although the upper and lower size ranges of lobsters were inadquately represented in the sample, the results showed that the number of eggs carried by a female increases in relation to an increase in carapace length ($r = 0.810$; $df = 33$; $P < 0.01$) (Table 1). The relationship between the number of eggs carried and carapace length (Figure 1) is expressed by the equation:

$$Y = -226399 + 5541.3X^* \qquad (2)$$

where X = carapace length in millimeters
Y = number of eggs carried

*Additional samples collected recently from females larger than 104.6 mm CL indicate that the relationship may be curvilinear.

TABLE 1. CARAPACE LENGTH AND THE ESTIMATED NUMBER OF EGGS CARRIED BY SPINY LOBSTER, *PANULIRUS MARGINATUS*, CAUGHT AT NECKER ISLAND AND MARO REEF

Carapace Length (mm)	Estimated No. of Eggs	Carapace Length (mm)	Estimated No. of Eggs
56.7	129,266	85.6	133,350
58.6	96,602	86.3	339,289
58.8	94,053	86.6	235,003
60.9	60,101	86.7	330,095
61.8	136,534	86.7	242,887
63.0	160,196	86.8	193,560
64.7	166,897	87.2	228,322
67.9	171,607	87.5	178,780
67.9	143,005	88.3	299,581
68.9	105,767	88.8	246,068
71.5	161,370	89.0	257,692
71.6	166,050	89.9	303,233
73.4	202,428	91.4	161,562
77.8	237,730	93.4	389,552
78.0	194,075	96.8	315,518
81.2	207,247	99.4	282,183
82.4	240,533	104.6	454,362

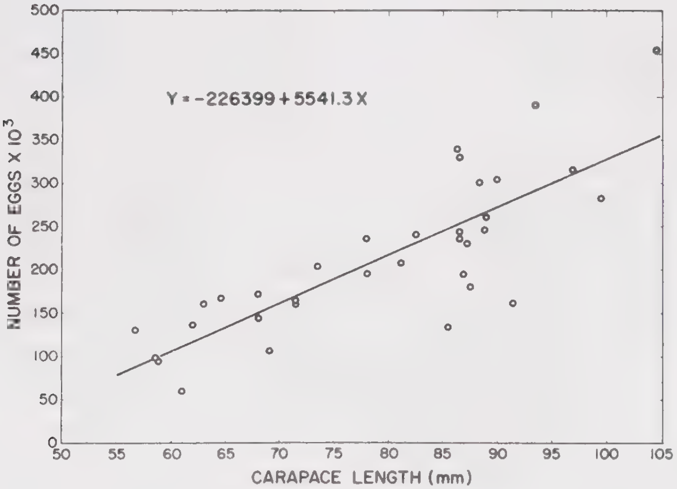

Figure 1. Relationship between the number of eggs carried and carapace length in the spiny lobster, *Panulirus marginatus*

DISCUSSION AND CONCLUSION

To determine whether the estimates obtained from this study differed from those provided by other investigators, comparisons were made for certain sizes for which estimates were available either in tabular form (Morris, 1968) or graphic form (McGinnis, 1972) (Table 2).

TABLE 2. CARAPACE LENGTH AND THE NUMBER OF EGGS CARRIED BY FEMALE *PANULIRUS MARGINATUS* AT OAHU, NECKER ISLAND, AND MARO REEF

Carapace Length (mm)	Estimated Number of Eggs Carried		
	Oahu*	Oahu†	Necker Island and Maro Reef§
54	--	--	72,831
69	134,000	--	155,951
70	--	140,000	161,492
80	--	210,000	216,905
81	261,000	--	222,446
83	228,000	--	233,529
87	271,000	--	255,694
89	280,000	--	266,777
90	--	280,000	272,318
93	328,000	--	288,942
95	263,000	--	300,024
98	--	--	316,648
100	--	410,000	327,731
101	440,000	--	333,272
101	431,000	--	333,272
101	467,000	--	333,272
102	--	--	338,814
102	--	--	338,814
105	495,000	--	355,438
110	--	575,000	--
111	--	--	--

*Data from Morris (1968).

†Data from McGinnis (1972).

§Data from this study and estimated by the regression equation.

Comparison of data from Morris (1968) with those obtained from this study showed rather good agreement at the lower size range. Morris estimated that a female of 83.0 mm CL caught off Oahu carried 228,000 eggs compared to an estimated 233,529 eggs carried by a female of similar size caught in the NWHI. At a larger size of 101 mm CL, however, the discrepancy was larger; this study estimated 333,272 eggs whereas Morris estimated from 431,000 to 467,000 eggs.

The egg counts for *P. marginatus* were also similar at the lower size range to counts obtained by McGinnis (1972) for specimens also caught around Oahu. For example, McGinnis found that *P. marginatus* of 70 mm CL produced about 140,000 eggs. In comparison, a 70-mm CL female in this study was estimated to carry 161,492 eggs. At larger sizes, however, the counts by McGinnis on Oahu lobsters were higher. His data showed that a 90-mm CL female carried about 280,000 eggs, whereas the equation calculated for this study predicts that at 90 mm CL, the number of eggs carried by a female is 272,318.

The estimates of the number of eggs carried obviously vary with the accuracy and precision of the sampling, weighing, and counting. Kensler (1967) found that the number of eggs in a gram sample can vary from 6,453 to 8,341 for *Jasus verreauxi*. Morgan (1972) reported that fecundity can be calculated with some degree of accuracy by basing egg counts on individual females and by not averaging counts based on several specimens of different sizes.

Apparently, *P. marginatus* is less fecund than other members of the genus. Berry (1971) showed that a 70 mm CL *P. homarus* of South African waters carried 309,907 eggs. Ino (1950) estimated that a 71 mm CL *P. japonicus* carried 524,000 eggs. Berry (1973) reported that a female *Palinurus delagoae* carried far fewer eggs for its size than any of the other members of Palinuridae. Apparently, the smaller number of eggs carried by the females of this species is associated with the comparatively large egg size. Berry added that like many other deepwater crustaceans, *P. delagoae* produces relatively few large eggs which have a prolonged incubation period. The extended incubation produces larvae which when hatched are in an advanced stage of development. Egg size, then, appears to be an important consideration when studying fecundity.

FUTURE RESEARCH NEEDS

Additional samples, particularly in the lower size ranges below 60 mm CL and in the upper size ranges beyond 90 mm CL, are needed to extend the range and improve the estimates already obtained. As more data are accumulated, comparisons will be possible to determine variations in fecundity estimates among the islands and banks sampled.

SUMMARY

Egg counts were made on 34 female *Panulirus marginatus* caught at Necker Island and Maro Reef. The smallest female (56.7 mm CL) carried an estimated 129,000 eggs whereas the largest female in the sample (104.6 mm CL) carried an estimated 454,000 eggs. The study also showed that the number of eggs carried increases relative to an increase in CL. A comparison of estimates of the number of eggs carried by female spiny lobsters caught off Oahu shows relatively good agreement with those obtained for the females caught at Necker Island and Maro Reef.

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Per Capita Annual Utilization and Consumption of Fish and Shellfish in Hawaii, 1970-77

LINDA L. HUDGINS

Introduction

In 1977, the U.S. per capita consumption of edible (meat-weight) fish and shellfish was 5.82 kg (12.8 pounds). It has been speculated that the per capita consumption of fishery products in the State of Hawaii is considerably higher than the U.S. average. No studies have been done to verify this speculation.

This paper is an attempt to quantify the actual consumption in Hawaii for the period 1970-77. This quantification required computation of the total supply of fish and fishery products available in Hawaii. The total supply was then adjusted to edible weight and divided by the population. The result is that the per capita consumption rate in Hawaii for 1977 was about 77 percent higher than the U.S. average.

Foreign imports represented, in 1977, approximately 54 percent of the total supply of fish and shellfish in Hawaii. Therefore, a section and tables are included in which these imports are disaggregated by quantity, value, and type of preparation for 1970-77; and by major product and major country of origin for 1976 and 1977.

An effort was made to calculate the per capita figures with the same methodology as that used in "Fisheries of the United States" (Bell, 1978) where national per capita estimates are published. The units of quantity and measurement in this report are not exactly comparable in some cases. These measurement discrepancies, as indicated in the table notes, should not hinder the usefulness of these preliminary estimates, however.

Data and Methods

The State of Hawaii has three major sources of commercial fish and fishery products for human consumption: 1) Local catch, 2) imports from foreign countries, and 3) interstate shipments from the mainland United States. Table 1 gives totals for these sources. Hawaii landings are shown in round (live) weight as reported by the vessels to the State of Hawaii, Division of Fish and Game. Foreign imports and interstate shipments are in net product weight, as recorded at the port by U.S. Customs officials and published by the U.S. Bureau of the Census (1970-77) and the U.S. Army Corps of Engineers (1970-77).

Hawaii per capita utilization of fish and shellfish (Table 2) is determined using total supply of fishery products without adjustment for beginning or ending stocks, foreign exports, or defense purchases. Table 3 gives a comparison of the United States and Hawaii per capita utilization rates. Table 4 gives U.S. per capita consumption of fish and shellfish as published by the National Marine Fisheries Service.

Hawaii per capita consumption in Tables 5-7 is based on pounds of edible (meat-weight) fish. Figures for Hawaii in Tables 5-7 are adjusted for foreign exports of fish and shellfish and shipments of canned tuna and fresh and frozen fish to the mainland United States. Supply of cured fish for consumption includes fish dried, salted, smoked, or kippered whether canned or not. Cured supply does not include local production of cured fishery products. Raw inputs for local production are counted under fresh, frozen, or chilled. Supply of canned fish for consumption includes fish of all preparations in airtight containers, most of which are cans.

Table 1.—Total Hawaii supply of commercial fish and shellfish, in thousands of pounds, by source and year, 1970-77.[1]

Year	Local commercial landings[2]	Foreign imports[3]	Interstate shipments[4]	Total
1970	11,282.3	22,960.3	5,896.0	40,138.6
1971	17,159.8	18,681.3	5,764.0	41,605.1
1972	14,754.7	28,953.6	4,682.0	48,390.3
1973	14,382.4	21,346.9	3,950.0	39,679.3
1974	11,323.7	24,467.2	4,068.0	39,858.9
1975	9,724.5	22,015.6	4,362.0	36,102.1
1976	15,272.3	19,846.3	4,094.0	39,212.6
1977	13,783.4	30,991.3	7,650.0	52,424.7

[1] Based on the total supply of edible fishery products, without taking into consideration beginning or ending stocks, exports, or defense purchases.

[2] State of Hawaii, Department of Land and Natural Resources, Division of Fish and Game. Reports in round weight.

[3] U.S. Bureau of the Census (1970-77). Reported in net product weight.

[4] U.S. Army Corps of Engineers (1970-77). Reported in net product weight.

The State of Hawaii has three variable components of population in addition to the civilian resident population: Military, visitors, and foreign immigrants. Military includes those who are serving in the armed forces and either actually residing in Hawaii or stationed aboard a ship homeported in Hawaii. Since 1971, the military has stabilized at around 6 percent of total de facto population (those actually present in the State). Military dependents are counted as part of the resident civilian population. There are approximately 1.15 dependents per military member in Hawaii. Visitor population, estimated by the Hawaii Visitors Bureau, during 1978 was around 9 percent of the total population based on the annual average number of visitors present. Approximately 8 percent of the civilian resident population of Hawaii in 1970 were

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Table 2.—Per capita utilization of commercial fish and shellfish in Hawaii by year, source of fish, and two population groups, 1970-77.

	Resident civilian and military population						Resident civilian, military, and visitor population				
				Per capita utilization					Per capita utilization		
Year	Total resident civilian and military population, 1 July (1,000 persons)[1]	Armed forces (1,000 persons)	Total Hawaii supply (1,000 lb)[2]	Local commercial catch	Interstate shipments and foreign imports	Total	Total resident civilian and military plus visitor population (1,000 persons)[1]	Visitors present (annual average) (1,000 persons)	Local commercial catch	Interstate shipments and foreign imports	Total
1970	775.6	53.2	40,138.6	14.5	37.2	51.7	803.4	37.6	14.1	35.9	50.0
1971	800.9	50.8	41,605.1	21.4	30.5	51.9	833.3	41.9	20.7	29.3	50.0
1972	823.3	52.0	48,390.3	17.9	40.9	58.8	865.9	51.3	17.0	38.9	55.9
1973	844.1	58.1	39,679.3	17.0	30.3	47.3	895.9	61.6	16.1	28.2	44.3
1974	855.4	57.5	39,858.9	13.2	33.4	46.6	913.6	66.0	12.4	31.2	43.6
1975	867.9	58.9	36,101.9	11.2	30.4	41.6	927.7	68.8	10.5	28.4	38.9
1976	883.5	57.8	39,212.6	17.3	27.1	44.4	952.7	78.5	16.0	25.2	41.2
1977	894.7	56.5	52,424.7	15.4	43.2	58.6	972.5	86.8	14.3	39.7	54.0

[1] Hawaii. Department of Planning and Economic Development (1978:6).

[2] Table 1, unadjusted for beginning and ending stocks, exports, or defense purchases. Excludes imports of nonedible fishery products.

Table 3.—United States and Hawaii total supply (million pounds) and per capita utilization (pounds) of commercial fish and shellfish by year, 1970-77.

	Total supply[1]		Total per capita utilization[2]	
Year	U.S.	Hawaii	U.S.[3]	Hawaii
1970	11,474	41.13	56.0	51.7
1971	11,804	43.11	57.0	51.9
1972	13,849	49.68	66.3	58.8
1973	10,378	40.94	49.3	47.3
1974	9,875	40.85	46.6	46.6
1975	10,129	36.95	47.4	41.6
1976	[4]11,555	40.55	53.7	44.4
1977	[4]10,579	53.63	48.8	58.6

[1]Total supply for U.S. includes nonedible and industrial fishery products not included in total supply for Hawaii.

[2]Population is total resident civilian and military population present on 1 July.

[3]Bell (1978:70).

[4]Preliminary.

Table 4.—United States per capita consumption of commercial fish and shellfish by year and three types of preparation, 1970-77.[1]

		Per capita consumption (lb)			
Year	Civilian resident population (million persons)	Fresh and frozen	Canned	Cured	Total
1970	201.7	6.9	4.5	0.4	11.8
1971	204.3	6.7	4.3	0.5	11.5
1972	206.5	7.2	4.9	0.4	12.5
1973	208.1	7.5	5.0	0.4	12.9
1974	209.7	7.0	4.8	0.4	12.2
1975	211.4	7.4	4.3	0.4	12.1
1976	[2]213.0	8.2	4.3	0.5	13.0
1977	[2]214.7	7.8	4.6	0.4	12.8

[1]Bell (1978:72).

[2]Preliminary.

Table 5.—Hawaii per capita consumption[1] of commercial fish and shellfish by year and three categories of preparation, 1970-77.

		Per capita consumption (lb)			
Year	Total civilian resident population 1 July (1,000 persons)	Fresh and frozen	Canned[2]	Cured[3]	Total
1970	722.6	19.4	5.3	1.0	25.7
1971	750.1	20.5	4.6	0.7	25.8
1972	771.3	17.1	6.6	0.8	24.5
1973	785.9	16.7	3.8	0.9	21.4
1974	797.9	14.0	4.7	0.6	19.3
1975	809.0	15.3	3.6	0.7	19.6
1976	825.7	15.3	4.3	0.8	20.4
1977	838.3	17.8	4.0	0.9	22.7

[1]Unadjusted for beginning and ending inventories and military purchases. Adjusted for exports to foreign countries from the Honolulu Customs district.

[2]Includes preserved and prepared which are canned but not included in cured

[3]Does not include local production.

Table 6.—Hawaii per capita consumption of commercial fish and shellfish by year and three types of preparation, 1970-77 including annual average visitor population.[1]

		Per capita consumption (lb)			
Year	Total civilian resident population plus visitors 1 July (1,000 persons)	Fresh and frozen	Canned[2]	Cured[3]	Total
1970	760.2	18.9	5.0	0.9	24.8
1971	792.0	19.4	4.3	0.7	24.4
1972	822.6	16.0	6.2	0.8	23.0
1973	847.5	15.5	3.5	0.9	19.9
1974	863.9	12.9	4.4	0.9	18.2
1975	877.8	14.1	3.4	0.6	18.1
1976	904.2	14.0	3.9	0.7	18.6
1977	925.1	16.1	3.6	0.8	20.5

[1]Unadjusted for beginning and ending inventories, and military purchases. Adjusted for exports from the Honolulu Customs district.

[2]Includes preserved and prepared which are canned but not included in cured.

[3]Does not include local production.

foreign born persons from the People's Republic of China, Taiwan, Japan, Korea, and the Philippines. All of these countries have substantially higher per capita fish consumption rates than that of the United States (Bell, 1978:74). These three components of population may account for over 20 percent of the actual population present in the State at a given time. For this reason, per capita consumption was calculated for various measures of population which would include these groups.

Table 7.—United States and Hawaii total per capita consumption (pounds) of commercial fish and shellfish by year, 1970-77.[1]

Year	Total per capita consumption U.S.	Total per capita consumption Hawaii[2]
1970	11.8	25.7
1971	11.5	25.8
1972	12.5	24.5
1973	12.9	21.4
1974	12.2	19.3
1975	12.1	19.6
1976	[3]13.0	20.4
1977	[3]12.8	22.7

[1] Population is total civilian resident population.
[2] Unadjusted for beginning and ending inventories and military purchases.
[3] Preliminary.

Foreign Imports

Imports from foreign countries in 1977 represented 54 percent of the total supply of fish, fishery products, and shellfish in Hawaii. Table 8 gives these imports by year and type of preparation, aggregated over countries. All of these products are designated for human consumption. Values are unadjusted and reflect customs values. Customs value generally represents a value in the foreign country, and therefore excludes U.S. import duties, freight, insurance, and other charges incurred in bringing the merchandise to the United States. This value may not reflect the actual transaction value.

Table 9 gives imports to Hawaii of fresh, frozen, or chilled fish and shellfish by major country of origin, quantity, and customs value. Relative rankings of these countries vary between 1976 and 1977. However, the major five countries (New Hebrides, Philippines, Taiwan, Japan, and Panama) are the same for both years. Fiji had no recorded exports to Hawaii in these categories for 1977.

Table 10 gives imports to Hawaii "in cans or airtight containers." Shellfish and anchovies are the major products. In 1972, the major sardine exporting countries were Brazil, United Kingdom, and Denmark. In 1973, only Denmark is recorded as exporting sardines to the Honolulu customs district which is reflected in the much lower 1973 figure. The category marked "other" in this and subsequent tables represents other species which the U.S. Customs aggregates under the heading "not elsewhere specified."

Table 8.—Foreign imports to Hawaii of fish and fish products for human consumption by year, type of preparation, quantity and customs value,[1] 1970-77.

	Total		Fresh, chilled, frozen		Cured		Fish in airtight containers		Fish products (pastes, balls, sticks, roe)		All shellfish	
Year	Quantity (1,000 lb)	Value ($1,000)	Quantity (1,000 lb)	Value ($1,000)	Quantity (1,000 lb)	Value ($1,000)	Quantity (1,000 lb)	Value ($1,000)	Quantity (1,000 lb)	Value ($1,000)	Quantity (1,000 lb)	Value ($1,000)
1970	22,906.3	10,354.8	19,417.9	6,376.9	81.1	78.4	422.1	215.5	481.7	374.8	2,557.5	3,309.2
1971	18,681.2	10,633.1	13,893.0	5,146.2	85.0	86.8	974.3	397.7	810.0	479.1	2,919.0	4,523.3
1972	28,953.6	15,755.6	23,693.8	9,816.9	85.8	147.0	1,317.9	497.3	1,123.5	609.3	2,732.8	4,685.1
1973	21,346.9	13,633.5	16,496.5	7,703.3	119.5	212.9	853.3	381.4	1,222.8	878.9	2,654.9	4,457.0
1974	24,467.2	17,303.3	19,340.0	10,182.8	113.4	145.3	767.5	501.6	1,342.7	854.2	2,903.6	5,619.4
1975	22,015.6	13,393.4	17,320.0	7,815.2	87.0	119.9	816.1	433.1	1,583.2	1,114.0	2,208.8	3,911.1
1976	19,846.3	14,185.4	14,917.3	7,380.1	131.0	163.3	877.3	500.5	1,634.0	1,118.4	2,286.7	5,023.1
1977	30,991.3	22,875.4	26,448.9	15,729.3	94.8	152.6	746.2	521.2	1,387.4	1,151.2	2,314.0	5,321.1

[1] Customs value generally represents a value in the foreign country, and therefore excludes U.S. import duties, freight, insurance, and other charges incurred in bringing the merchandise to the United States. This value may not reflect the actual transaction value. These values are unadjusted.

Table 9.—Imports of fresh, frozen, chilled fish and shellfish by major countries of origin,[1] quantity, and customs value,[2] 1976 and 1977.

	1976		1977	
Country of origin	Quantity (1,000 lb)	Customs value ($1,000)	Quantity (1,000 lb)	Customs value ($1,000)
Fish				
New Hebrides	6,016.9	3,216.3	19,014.7	11,991.0
Philippines	23.6	19.5	3,345.9	865.4
Taiwan	1,876.1	1,411.3	2,749.4	2,019.6
Japan	1,070.7	742.1	727.2	534.2
Panama	3,856.0	1,104.0	165.5	55.7
Fiji	1,180.0	538.7	—	—
Shellfish				
New Zealand	248.1	1,407.9	213.0	1,514.0
Taiwan	134.7	457.5	93.6	369.0
Japan	42.3	129.3	18.6	61.4

[1] Country of origin as determined by U.S. Customs.
[2] See footnote 1, Table 8.

Table 10.—Foreign imports to Hawaii of fishery items, canned and in airtight containers, all manner of preparation, net weight in thousand pounds, 1970-77.

Year	Salmon	Sardines	Tuna	Anchovies	Shellfish	Other	Total
1970	18.6	45.0	95.0	54.6	1,323.6	208.9	1,745.7
1971	45.9	182.5	85.6	153.3	1,218.7	507.0	2,193.0
1972	68.2	389.5	55.2	228.4	1,247.0	576.6	2,564.9
1973	([1])	26.9	78.7	242.1	1,225.5	506.0	2,079.2
1974	11.6	21.8	120.0	213.1	1,898.8	401.0	2,666 3
1975	([1])	6.5	112.0	358.5	1,315.9	339.0	2,131.9
1976	([1])	34.3	139.3	355.7	1,319.8	348.0	2,197.1
1977	11.6	44.2	29.6	305.3	1,243.4	355.5	1,989.6

[1] None reported.

Table 11 reflects edible fishery products by major type of preparation. Tuna, fish fillets, and shellfish compose over 90 percent of the total fresh and frozen imports to Hawaii for 1976 and 1977. The itemized entries under "canned" for 1976 reflect over 60 percent of the total quantity of canned imports to Hawaii and for 1977 over 78 percent. The category "Other fish and shellfish" reflects the sum over type of preparation of the "not elsewhere classified" specifications.

Table 12 represents estimated per capita consumption of foreign imports by type of preparation, adjusted to pounds of edible fishery products divided by civilian resident population of Hawaii on 1 July of each year.

Table 11.—Foreign imports of edible fishery products to Hawaii, by principal items, 1976 and 1977.

Item	1976 1,000 lb	1976 $1,000[1]	1977 1,000 lb	1977 $1,000[1]
Fresh and frozen				
Tuna				
Albacore	5,177.6	2,980.8	14,959.8	10,183.9
Skipjack	2,200.2	627.5	2,343.7	598.7
Yellowfin	4,136.3	1,507.9	5,287.8	2,158.9
Fillets	2,494.1	1,832.1	3,253.1	2,358.4
Shellfish				
Clams	29.2	27.8	17.3	26.6
Lobsters	297.6	1,619.8	245.5	1,654.9
Shrimp and prawns	242.9	779.2	137.5	486.9
Other	948.6	551.5	637.4	576.2
Canned				
Salmon	0	0	11.6	22.6
Anchovies	355.7	94.0	305.3	94.4
Sardine				
Not in oil	23.9	8.0	43.7	25.3
Tuna	139.3	128.3	29.6	35.2
Bonito and yellowtail	3.1	7.5	2.2	6.1
Clams	182.1	234.0	174.8	275.7
Shrimp	31.4	57.9	50.5	104.9
Other	510.0	549.5	474.4	768.4
Cured				
Pickled, salted, or dried	577.8	1,078.5	719.2	1,278.6
Smoked or kippered	81.3	80.5	57.1	80.4
Other fish and shellfish	2,415.2	2,020.6	2,240.8	2,139.1
Total edible fishery products	19,846.3	14,185.4	30,991.3	22,875.2

[1] See footnote 1, Table 8.

Table 12.—Estimated Hawaii per capita consumption of foreign imports of fish, fishery products, and shellfish by year and type of preparation, 1970-77.[1]

Year	Total civilian resident population, July 1 (1,000 persons)	Per capita consumption (lb) Fresh, chilled, frozen[2]	Dried, salted, pickled, smoked, kippered	Fish in airtight containers	Pastes, balls, sticks	Shellfish	Total
1970	722.6	6.2	0.1	0.6	0.7	0.5	8.1
1971	750.1	4.8	0.1	1.3	1.1	0.7	8.0
1972	771.3	5.5	0.1	1.7	1.5	0.7	9.5
1973	785.9	5.0	0.2	1.1	1.6	0.5	8.4
1974	797.9	3.4	0.1	1.0	1.7	0.4	6.6
1975	809.0	4.7	0.1	1.0	2.0	0.4	8.2
1976	825.7	3.8	0.2	1.1	2.0	0.4	7.5
1977	838.3	2.0	0.1	0.9	1.7	0.3	5.0

[1] Unadjusted for exports, defense purchases, or beginning or ending stocks

[2] Based on imported weight which is net product weight. In some cases this is meat-weight; in others, this is whole or round weight. Customs reports only net product weight.

Summary and Conclusions

The tabulated data show that the total per capita consumption of fish and shellfish in the State of Hawaii has been higher than the U.S. average over the entire period 1970-77. Specifically, the following conclusions can be drawn about fish and shellfish consumption:

1) United States per capita total consumption has followed a slight upward trend—from 1973 to 1977, consumption varied between 5.45 and 5.91 kg (12 and 13 pounds).

2) Hawaii per capita consumption for all fish products followed an unclear trend over the period. Consumption declined dramatically from 1972 [11.14 kg (24.5 pounds)] to 1974 [8.77 kg (19.3 pounds)] and has since followed a solid upward trend.

3) Per capita consumption of fresh and frozen fishery products in Hawaii has ranged from 206 percent (in 1971) to 87 percent (in 1976) above the national average.

4) Per capita consumption of canned fishery products in Hawaii since 1973 has been below the U.S. average.

5) Per capita consumption of cured fishery products in Hawaii has been above the U.S. average for the period. Since this does not include local Hawaii production, the cured fishery products consumption rate in Hawaii is actually higher than the data indicate.

These results show that the most pronounced decline in the 1972-74 period occurred in the fresh and frozen category. During this time, factors which may have possibly caused the decline were: 1) A change in tastes due to the public concern over high mercury content in large pelagic fishes. Market observers during this period report that the local fishermen were unable to sell many of their fish and that it is conceivable it would have taken several years for the consumers to return to their higher preference levels for fish. 2) The observed reduction in the quantity of local supply during 1972-74 was possibly a result of a decline in demand due to a change in tastes. 3) At the same time (1972) the visitor population began to grow much faster (12.2 percent annually) than the civilian resident population (2.1 percent annually). This visitor population may exhibit differential consumption rates that are higher or lower than the resident population. However, any effect other than an absolute increase in the population is indeterminant. A diminished supply of fresh fish combined with a larger population base would result in a lower observed per capita consumption rate.

Hawaii has a large recreational fishery. The decline in the fresh category may be modified when consumption by recreationalists that is not reported in the commercial catch is taken into consideration. Yearly data for recreational landings as a separate category are not available. A recent study[1] used Kailua-Kona, Hawaii, survey information to estimate gamefish catch by commercial and recreational troller vessels for 1976. The authors' "Estimate I" (Table 4) represents an adjustment to statewide Division of Fish and Game data which accounts for underreporting and differential vessel catch rates by vessel category. When this estimate was considered, the total Hawaii supply of fish and fishery products (for 1976) increased from 17,829,909.1 kg (39,212,600 pounds) to 18,432,090.9 kg (40,550,600 pounds), per capita consumption of fresh and frozen fish increased from 6.95 kg (15.3 pounds) to 7.32 kg (16.1 pounds), and total Hawaii per capita consumption increased from 9.27 kg (20.4 pounds) to 9.64 kg (21.2 pounds).[2] Consumption of canned and cured fish are unaffected. It should be noted that the above estimate should therefore be considered as an approximation of one component of total recreational catch, that component caught by troller vessels and sold. Recreational catch that is not sold does not have to be reported.

Estimates of per capita consumption rates and the trends of these rates provide valuable input to research and policy planning. Specific determinants of this consumption have not been addressed here. However, these results have implications in particular for the Hawaii fishing industry, the aquaculture development program in Hawaii, the State of Hawaii Fisheries Development Plan, and Regional Fishery Management Plans.

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[2] Population is total resident civilian.

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FEEDING HABITS OF THE KAHALA, *SERIOLA DUMERILI*, IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

Stomach contents of kahala, *Seriola dumerili*, were examined for a determination of possible relationships between the feeding habit and incidence of ciguatoxicity in this species and also as part of a study on its overall life history. Preliminary results indicated a change from cephalopods to fish as the principal dietary constituent with increase in weight of kahala. Also, the diet of fish caught in the Northwestern Hawaiian Islands appeared more varied in terms of a larger combined cephalopod and crustacean volume than those caught in two other areas within the main islands. Fish dominated the diet of kahala, with Carangidae the largest contributor among forage items. High incidences of parasitic nematodes and trematodes were observed with nematodes the most predominant in occurrence. Further examination of stomach contents is needed to ascertain the dietary trends indicated thus far.

Northwestern Hawaiian Islands
Seriola dumerili
ciguatera
stomach analysis

INTRODUCTION

The kahala, *Seriola dumerili* (Risso), is found worldwide and its Indo-Pacific distribution reaches Hawaii, Australia, Japan, China, and eastern Africa (Mather and Bartlett, 1966). Within the Hawaiian Archipelago, kahala is found primarily in 40 to 100-fathom depths within coastal waters and it appears to be primarily associated with the bottom (Gosline and Brock, 1960).

Food habit studies on members of Seriola are few. The feeding habits of pelagic larval and juvenile stages of Seriola quinqueradiata were studied in waters off Kyushu, Japan. The diet consisted primarily of planktonic crustaceans and the larvae and juvenile stages of Engraulidae, Scomberesocidae, and Mullidae (Anraku and Azeta, 1965). Studies on the yellowtail, Seriola dorsalis, in California indicated that this species was an "opportunistic feeder," its diet consisting mainly of pelagic red crabs, squid, sardines, anchovies, jack mackerel, Trachurus symmetricus, and Pacific mackerel, Scomber japonicus (Baxter, 1960). No published food habit studies are available for kahala found in Hawaiian waters or elsewhere.

The objectives of the current food habit study on kahala are twofold: (1) to determine whether differences in forage items exist in the diets of ciguatoxic and non-ciguatoxic fish in conjunction with the current ciguatoxin study of kahala and, (2) to investigate the food habits as part of an overall life history study of this species.

METHODS

Stomachs are collected along with gonads and flesh samples as part of an ongoing ciguatoxin study of kahala. A cooperative program was established by which fishermen and fish dealers send all kahala to the fish auction house located at the United Fishing Agency (UFA). Sampling is conducted by National Marine Fisheries Service employees six days a week on all kahala sent to UFA. Data are collected on weight, fork length, sex, depth, and location of capture for each fish.

The samples are processed at the University of Hawaii John A. Burns School of Medicine, Pathology Department, with a practical and relatively specific radioimmunoassay (RIA) for the detection of ciguatoxin (Hokama et al., 1977). The toxicity levels of the fish tissues are determined from radioactive counts per minute per gram tissue (c/min/g) as follows: <350,000 c/min/g tissue - negative; 350,000 to 399,999 c/min/g tissue - borderline: and ≥400,000 c/min/g tissue - positive.

Because stomachs are not preserved at time of capture, there is a lag time of one to ten days before stomachs are collected and preserved. Collected stomachs are placed in a cloth bag and preserved in 10% formaldehyde until time of examination.

For detailed examination, stomach contents are emptied and sorted into identifiable groups. The volume of each food item is measured (by water displacement) and coded as to its state of digestion. Invertebrates were usually identifiable to suborder whereas most fish were identifiable to family and occasionally to species. Unidentified fish were cleaned of flesh and stained in alizarin for identification via vertebrae count and morphology.

Bait is usually identifiable by its appearance (sliced fish sections) and its minimal state of digestion. Food items suspected as bait are recorded but not considered actual food items. Additionally, all nematodes and trematodes collected from stomachs are recorded and preserved but are considered to be parasites and not food items.

RESULTS

The percentage of frequency of occurrence and total volume of each food item indicated that the major categories of food consumed by kahala consisted of Crustacea, Cephalopoda, and other Mollusca, fish, and unidentified remains. Diet was analyzed in relation to ciguatoxicity, sex, location of capture, and weight.

Ciguatoxicity versus diet

No apparent differences in the major food categories appear between ciguatoxic and non-ciguatoxic kahala examined. Fish appeared frequently and predominated in volume for both groups. Among ciguatoxic individuals, fish contributing the most by volume were Carangidae, Tetraodontidae, and unidentified fish remains; whereas, for non-ciguatoxic fish Carangidae, Scombridae, and unidentified fish remains were the major contributors (Tables 1 and 2).

TABLE 1. NUMBER, FREQUENCY OF OCCURRENCE, AND VOLUME OF FORAGE ITEMS FOUND IN STOMACHS OF 29 CIGUATOXIC KAHALA

Food Items	No. of Items	Stomachs in Which Occurred		Aggregate Total Volume	
		Number	Percent	Milliliter	Percent
Crustacea					
Unidentified shrimp	2	1	3.4	--	--
Fish					
Carangidae					
Decapterus sp.	1	1	3.4	18	5.5
Trachurops crumenophthalmus	1	1	3.4	66	20.3
Mullidae	1	1	3.4	2.0	0.6
Balistidae	1	1	3.4	13	4.0
Tetraodontidae	35	3	10.3	60.0	18.4
Unidentified fish larva	1	1	3.4	--	--
Unidentified fish	5	4	13.8	10.6	3.3
Unidentified fish remains	--	6	20.7	59.5	18.3
Unidentified remains	--	22	75.9	96.2	29.6
Parasites					
Trematodes	40	11	37.9	--	--
Nematodes	152	10	34.5	--	--

TABLE 2. NUMBER, FREQUENCY OF OCCURRENCE, AND VOLUME OF FORAGE ITEMS FOUND IN STOMACHS OF 125 NON-CIGUATOXIC KAHALA

Food Items	No. of Items	Stomachs in Which Occurred		Aggregate Total Volume	
		Number	Percent	Milliliter	Percent
Annelida					
Unidentified	12	4	3.2	--	--
Crustacea					
Isopoda	2	2	1.6	0.3	--
Decapoda					
Heterocarpus ensifer	21	1	0.8	8.3	0.1
Unidentified penaeid shrimp	5	2	1.6	6.6	0.1
Unidentified caridid shrimp	1	1	0.8	0.5	--
Unidentified shrimp	148	2	1.6	59.9	0.9
Unidentified shrimp remains	--	1	0.8	52	0.8
Crab megalops	1	1	0.8	0.1	--
Unidentified Crustacea	5	3	2.4	0.3	--
Unidentified Crustacea remains	--	1	0.8	0.1	--
Mollusca					
Unidentified gastropod	2	1	0.8	--	--
Unidentified Bivalvia remains	--	2	1.6	1.8	--
Squid	17	7	5.6	51.3	0.8
Octopus	7	6	4.8	135.5	2.1
Unidentified Cephalopoda	6	4	3.2	10.7	0.2
Unidentified Cephalopoda remains	--	1	0.8	11.4	0.2
Fish					
Congridae	3	3	2.4	74.3	1.2
Antigoniidae	3	2	1.6	19	0.3
Fistulariidae	2	1	0.8	6.1	0.1
Carangidae					
Decapterus pinnulatus	4	4	3.2	449	7.0
Decapterus sp.	20	14	11.2	1,107.8	17.3

TABLE 2. NUMBER, FREQUENCY OF OCCURRENCE, AND VOLUME OF FORAGE ITEMS FOUND IN STOMACHS OF 125 NON-CIGUATOXIC KAHALA (Continued)

Food Items	No. of Items	Stomachs in Which Occurred		Aggregate Total Volume	
		Number	Percent	Milliliter	Percent
Trachurops crumenophthalmus	4	2	1.6	133	2.1
Unidentified	3	3	2.4	115	1.8
Unidentified remains	--	4	3.2	177	2.8
Lutjanidae					
Pristipomoides sieboldii	2	2	1.6	406	6.3
Unidentified	2	2	1.6	50	0.8
Mullidae	1	1	0.8	4.0	0.1
Labridae	2	2	1.6	22	0.3
Scombridae					
Auxis sp.	4	3	2.4	843	13.1
Auxis thazard	1	1	0.8	547	8.5
Monacanthidae					
Pseudomonacanthus garretti	5	1	0.8	218	3.4
Unidentified	8	3	2.4	116.8	1.8
Unidentified remains	--	1	0.8	1.3	--
Ostraciontidae					
Unidentified remains	--	1	0.8	6.8	0.1
Tetraodontidae	6	6	4.8	116.6	1.8
Unidentified flatfish	1	1	0.8	4.7	0.1
Unidentified fish	46	20	16.0	83.3	1.3
Unidentified fish remains	--	43	34.4	799.6	12.5
Unidentified squid and fish remains	--	1	0.8	5.6	0.1
Unidentified remains	--	65	52.0	772.6	12.0
Parasites					
Trematodes	183	33	26.4	--	--
Nematodes	2,757	92	73.6	--	--

Among ciguatoxic fish, nematodes and trematodes occurred in approximately 35% of the stomachs; whereas, among non-ciguatoxic fish, nematodes and trematodes occurred in approximately 75% and 25% of the stomachs, respectively.

Sex versus diet

Both sexes appear identical in their diet of major food categories; fish predominated followed by small amounts of cephalopods and crustaceans. Among both sexes, most of fish by volume were Carangidae and Scombridae.

The incidence of nematodes and trematodes between the sexes were very similar. Nematodes occurred in the stomachs two to three times more often than trematodes.

Location versus diet

Diet comparisons were made for fish from three areas: the island of Hawaii and the Molokai-Lanai-Maui-Kahoolawe area among the main islands, and Gardner Pinnacles in the Northwestern Hawaiian Islands. The frequency of occurrence of major food items among the three areas appear very similar. Kahala from both the island of Hawaii and the Molokai-Lanai-Maui-Kahoolawe area had a high content of fish and rather low content of crustaceans or cephalopods. For kahala from Gardner Pinnacles, fish were still predominant in volume although to a lesser extent than for kahala from the other two areas. The former had a larger volume of cephalopods and crustaceans and the volume of unidentified remains also was larger.

For kahala from the island of Hawaii the major fish contributors by volume were the Scombridae and Carangidae. In kahala from the Molokai-Lanai-Maui-Kahoolawe area the Carangidae and Lutjanidae predominated in volume and from those in the Gardner Pinnacles area, Monacanthidae, unidentified fish remains, and Carangidae predominated. Octopus was the only cephalopod.

Occurrence of nematodes and trematodes was very similar among fish in the three areas; nematodes occurred in approximately 75% of the stomachs and trematodes in about 25%.

Weight versus diet

The kahala were divided into three groups according to weight: <5.4 kg (12 lb), 5.4 to 10.0 kg (12 to 22 lb), and >10.0 kg (22 lb).

The volumetric data showed that the lighter weight group had a smaller percentage of fish compared to the two heavier groups. The lighter group showed a larger proportion of cephalopod compared to the other two groups which showed a predominance of fish. Octopus comprised practically all the cephalopods and Tetraodontidae contributed most of the fish for the first group. In the 5.4 to 10.0 kg group Carangidae and unidentified fish remains contributed the bulk of the fish whereas in kahala >10.0 kg the fish species consisted chiefly of Scombridae and Carangidae.

In the two groups >5.4 kg, nematodes and trematodes occurred in approximately 75% and 25% of the stomachs, respectively. Among fish in the lighter weight group, nematodes and trematodes occurred in 17% and 39% of the stomachs, respectively.

CONCLUSION

Preliminary results show no relation between toxicity, diet, and sex among kahala examined thus far. There appears to be some relationship though between diet and location of capture; fish from Gardner Pinnacles apparently have a more varied diet (a greater proportion of combined cephalopod and crustacean volume) than those from the island of Hawaii and the Molokai-Lanai-Maui-Kahoolawe area. Dietary differences are also indicated in comparisons of weight versus diet which show a greater volume of cephalopods for fish <5.4 kg and a changeover to fish as the major dietary component in larger kahala. Hence, except for the younger kahala, fish is the principal diet of kahala. Carangidae was the most frequently occurring family in terms of percentage of occurrence and total volume. Results to date reflect only trends in the data and should be considered only preliminary because of the small sample sizes.

The incidence of parasitic nematodes and trematodes were high in the stomachs of kahala; nematodes and trematodes were present in approximately 75% and 25%, respectively, of stomachs examined, regardless of sex and location of capture. In the ciguatoxic group and the group comprising fish <5.4 kg, trematodes were more abundant than nematodes. With the exception of the two above-mentioned groups, nematodes were the predominant parasite.

FUTURE RESEARCH NEEDS

Further analysis of stomach contents is needed to confirm the trends in dietary composition and incidence of parasites. Because only 15% of the kahala stomachs collected have so far been examined it should be emphasized that the results are preliminary. As more stomachs are examined other relationships will be investigated such as the consistency of diet over time, prey size in relation to fish weight, and various combinations of factors such as weight and location versus diet. Also, as more samples are processed, it may be possible to identify other food items, especially fish, that presently remain unidentified.

SUMMARY

One hundred and fifty-four stomachs collected from kahala, *Seriola dumerili*, representing 15% of the stomachs collected to date, were examined to determine a possible relationship between feeding habits and incidence to ciguatoxicity and as part of an overall study of the life history aspects of commercially valuable fishes in the Hawaiian Archipelago. Preliminary results indicate a change from cephalopods to fish as the principal food item with increase in size. In general, members of the family

Carangidae were the most important contributors among forage items for kahala. The results also indicated no apparent differences in the major food categories between ciguatoxic and non-ciguatoxic fishes and between sexes. Among sampling sites, however, differences were noted in volumes of cephalopods and crustaceans consumed.

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REPRODUCTIVE ECOLOGY OF WESTERN GULLS AND XANTUS' MURRELETS WITH RESPECT TO FOOD RESOURCES IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Western Gull (*Larus occidentalis*) and Xantus' Murrelet (*Endomychura hypoleuca*) reproduction on Santa Barbara Island, California, showed considerable sensitivity to changes in pelagic fish populations in the Southern California Bight. Western Gulls responded to decreases in the availability of schooling fish by failing to breed or by switching to alternate foods. The use of alternate foods may result in lower growth rates and chick survival. Timing of breeding was not significantly changed. Xantus' Murrelets foraged on larval fish, particularly larval northern anchovies (*Engraulis mordax*). Murrelets responded to the unavailability of larval anchovies either by failing to breed or by delaying breeding until larval anchovies became available. Our results demonstrate not only the sensitivity of marine bird reproduction as an indicator of the availability of their food resources, but also how specific differences in reproductive biology influence the flexibility of response to environmental change.

RESUMEN

La reproducción de la gaviota del oeste (*Larus occidentalis*) y el arán de Xantus (*Endomuchura hypoleuca*) en la Isla de Santa Bárbara, California, presentaron gran sensibilidad a los cambios en las poblaciones de peces pelágicos en la Bahía del Sur de California. Las gaviotas no criaron o variaron su régimen alimenticio cuando se produjo un descenso en la abundancia de peces en los cardúmenes. Al utilizar otros alimentos se puede producir una disminución en el índice de crecimiento y en la supervivencia de los polluelos. El tiempo de crianza no cambió significativamente. El arán de Xantus se alimentaba de larvas de peces, particularmente de anchoveta del norte (*Engraulis mordax*). Cuando hubo una escasez de larvas de anchoveta, el arán no lograba criar o retrazaba la época de cría hasta que las larvas de anchoveta eran abundantes. Nuestros resultados muestran no sólo la sensibilidad de la reproducción de aves marinas como un indicador de la disponibilidad de sus recursos de comida, sino también muestran cómo las diferencias especificas en la biología de reproducción influyen en la flexibilidad de respuestas a cambios en el medio ambiente.

INTRODUCTION

Ashmole (1963) hypothesized that "... short term and even slight fluctuations in the availability of food . . ." would have " . . . a profound effect on the breeding success in a particular season . . ." for tropical seabirds. He documented a number of cases in which reproductive success was diminished by chick mortality due to starvation. Harris (1978) also discussed the impact of food availability on temperate-breeding Common Puffins (*Fratercula arctica*). He found that supplemental feedings allowed chicks to grow faster and attain a heavier weight, and he suggested that these extra reserves of fat could be of survival value in brief episodes of food shortage.

Other workers have found that changes in food availability may affect not only reproductive success but also the number of birds attempting to breed. In both the guano industries of South Africa and of Peru, declines in fish abundance have been reflected by declines in the number of adult birds attempting to breed (Crawford and Shelton 1978; Jordan 1967; Murphy 1973). Ainley and Lewis (1974) also suggest that certain bird populations on the Farallon Islands, California, have been reduced due to the demise of the Pacific sardine (*Sardinops caerulea*), but their evidence is mostly circumstantial.

Evidence that fluctuations in the availability of a single food species might have a significant impact on the reproductive biology of a presumably generalized forager was presented by Hunt and Hunt (1976b). They found in Western Gulls (*Larus occidentalis*) nesting on Santa Barbara Island, California, a strong inverse correlation between the percent of chicks found empty and the percent of chicks containing anchovies in any one day's sampling. Gull chick survival is linked to food not only through starvation, but more importantly through behavioral differences in satiated and hungry chicks (Hunt and McLoon 1975; Hunt and Hunt 1976a).

We here examine the foraging preferences of two species of seabirds, the Western Gull and the Xantus' Murrelet and the effect of changes in northern anchovy availability on their reproduction at Santa Barbara Island. In particular, we show that as the availability of anchovies fluctuates, Western Gulls on Santa Barbara Island have different responses to these changes than Xantus' Murrelets nesting on the same island.

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METHODS

To measure the impact of changes in prey availability on seabird reproductive ecology, it is necessary to determine prey availability or abundance, the number of birds attempting to breed, and their reproductive performance. Three measures of reproductive are phenology, chick growth rates, and the number of chicks surviving to some age or weight criterion.

The number of Western Gulls attempting to nest on Santa Barbara Island was determined by direct counts of incubating and territorial gulls. Counts were made during the incubation period from a series of vantage points that allowed us to enumerate all nesting birds. Counts were repeated as often as once per week in some years to insure accuracy. Xantus' Murrelet numbers were not censused with sufficient accuracy to allow a quantitative assessment of their numbers. However, qualitative assessments of changes in abundance were made by individuals studying murrelet biology around the periphery of Santa Barbara Island.

The reproductive phenology of Western Gulls was measured on the major portion of Western Gull population in 1972 and 1974, and in 1975-77 in five 100 x 100-m grids on the west side of the Island. By concentrating our efforts consistently in these five grids, we avoided the potential problems of variability in the age or experience of the gulls biasing our year-to-year comparisons. Although formal study quadrants were not set up for Xantus' Murrelets, the same areas were used for study each year. Breeding phenology of Western Gulls and Xantus' Murrelets was determined by checking staked nests at least once every four days. In some years checks were made more frequently.

Growth rates of gull chicks were calculated using the slope of the linear portion of the growth curve (Spaans 1971; Hunt 1972; Hunt and Hunt 1975, 1976a) that occurs when Western Gull chicks weigh between 125 and 600 g. Weights were checked approximately once every four days. Xantus' Murrelet chicks are not fed in the short interval between hatching and their departure to sea, so growth rates could not be obtained for this species.

Gull chicks were recorded as surviving when they attained a weight of 500 g. Xantus' Murrelet chick survival is not relevant to the present study, as the major source of their mortality is predation by mice (Hunt et al. 1979).

Samples of food used by Western Gulls were obtained from chicks when they voluntarily regurgitated material during handling for banding or weighing. Occasionally samples were extracted by inserting an index finger down a chick's throat and withdrawing the contents of the proventriculus (Hunt 1972). Samples were obtained from chicks of all sizes and throughout the period when chicks were present on the Island. Most samples were obtained before 1000 or after 1600 in order to avoid subjecting chicks to heat stress during midday. Except for 1972, when samples were identified in the field (Hunt and Hunt 1976b), food samples were preserved and subsequently identified in the laboratory. Since anchovies appear to be a preferred food in the diet of Western Gulls at Santa Barbara Island, the percent weight or percent occurrence of anchovies in the diet of chicks is assumed to be a measure of their availability to foraging Western Gulls.

A second method for estimating changes in the abundance, and presumably the availability of anchovies, was to compare the year-to-year changes in the tonnage of anchovies reported by commercial fish spotters (Squire 1972). An index of northern anchovy abundance was calculated on the estimated total tons of anchovies reported by commercial spotters for daytime flights during the first and second quarters of each year, divided by the number of times pilots flew through the foraging areas used by Western Gulls nesting on Santa Barbara Island. The foraging area was determined from studies of radio-tagged and color-banded gulls reported in Hunt et al. (1979).

RESULTS

Adult Western Gulls feed their chicks by regurgitating food to them at the nesting territory. Western Gulls in the Southern California Bight use a wide variety of foods (Table 1). Foods used varied from colony to colony, presumably depending upon what was consistently most readily available near the colony. Likewise for a given colony, the types of foods used varied from year to year, again presumably reflecting changes in availability (Tables 2-4).

On Santa Barbara Island, not only do we have a longer time period over which sampling has been done, but also we have obtained considerable independent data on anchovy availability and reproductive success. From Table 4 it is clear that Santa Barbara Island Western Gulls depend primarily on fish, and to a lesser extent on the market squid, *Loligo opalescens*. These gulls did not make extensive use of intertidal organisms, and in only one year, 1976, did sea lion (*Zalophus californicus*) placentae or garbage and offal constitute a significant portion of their diet.

The species of fish taken by the Western Gulls on Santa Barbara Island have varied from one year to another. Most striking is the marked decline in the use of northern anchovies from a high of 42% of the diet in 1972 to a low of 18% in 1977. Alternative species taken have included Pacific saury, *Cololabis saira*, and the market squid. Only in 1976, when apparently there were no alternative marine species available, did gulls resort to using sea lion placentae and garbage, the availability of which is unlikely to change from one year to the next.

Over the course of the study, not only has the percentage of anchovies fed to gull chicks declined, but also the number of pairs laying eggs at Santa Barbara Island has decreased (Figure 1). This drop in the number of nesting birds has paralleled a decline in the amount of anchovies seen during daytime surveys in the first quarter of the year by commercial spotter pilots (Anchovy Stock Index; Figure 1). The correlation between numbers of breeding gulls and the Anchovy Stock Index is statistically significant ($r = 0.97$, $N = 4$). Given the relative importance of anchovies to the reproductive biology of this population of Western Gulls, it is reasonable to assume that changes in the yearly availability of anchovies influence the number of gulls attempting to breed.

The amount of anchovies fed to chicks also correlates with the abundance of anchovies (Figure 2), although in an unanticipated way. There is a very strong correlation ($r = 1.00$, $N = 4$) between the percentage of anchovies in the chick diets and the log of the Anchovy Stock Index for the first quarter of the year, during which gulls are preparing to nest. There is no statistically significant correlation between the Anchovy Stock Index during the second quarter when nesting and chick growth is occuring and the percentage of anchovies in the diets of chicks ($r = 0.33$, $N = 4$).

Gull chick survival has been correlated with growth rates in this study (Figure 3; $r = 0.99$, $N = 4$) and other

TABLE 1

Foods Commonly Fed to Western Gull Chicks, 1975-77

	Percent by occurrence			
Island	Prince	San Nicolas	Santa Barbara	Anacapa
N	87	76	250	36
Food type				
Euphausiacea	0	7	4	0
Loligo opalescens	21	15	4	3
other Cephalopods	7	1	2	8
other mollusks	0	9	1	0
Engraulis mordax	5	14	24	11
Porichthys notatus	2	4	1	3
Merluccius productus	5	1	3	3
Cololabis saira	1	1	30	8
Atherinops affinis				
Sebastes sp.	14	9	6	17
Perciformes	1	5	2	25
unidentified and other fish	45	29	15	31
all fish	68	63	81	98
sea lion placenta	3	18	4	0
garbage and offal	7	3	6	14

TABLE 2

Food Commonly Fed to Western Gull Chicks, Prince Island

	Percent by weight		
Year	1975	1976	1977
N	26	27	34
Food type			
Euphausiacea	1	0	0
Loligo opalescens	58	7	28
other Cephalopods	0	1	4
other mollusks	0	0	0
Engraulis mordax	0	21	0
Porichthys notatus	0	16	0
Merluccius productus	0	3	19
Cololabis saira	0	2	0
Atherinops affinis	0	0	0
Sebastes sp.	0	13	8
Perciformes	0	5	2
unidentified and other fish	30	22	17
all fish	30	82	46
sea lion placenta	3	3	0
garbage and offal	8	7	25
other	0	1	0

TABLE 3

Foods Commonly Fed to Western Gull Chicks, San Nicolas Island

	Percent by weight		
Year	1975	1976	1977
N	21	39	15
Food type			
Euphausiacea	0	6	0
Loligo opalescens	9	18	26
other Cephalopods	0	6	3
other mollusks	0	6	0
Engraulis mordax	16	22	0
Porichthys notatus	0	6	4
Merluccius productus	0	0	14
Cololabis saira	0	0	0
Atherinops affinis	0	13	6
Sebastes sp.	0	3	3
Perciformes	0	3	0
unidentified and other fish	59	2	13
all fish	75	49	40
sea lion placenta	14	16	10
garbage and offal	0	0	13
other	0	1	8

TABLE 4

Foods Commonly Fed to Western Gull Chicks, Santa Barbara Island

	Percent by weight			
	1972	1975	1976	1977
N	157	18	79	153
Food type				
Euphausiacea	0	0	0	0
Loligo opalescens	12	8	4	3
other Cephalopods	0	0	2	1
other mollusks	0	2	0	0
Engraulis mordax	45	32	28	18
Porichthys notatus	2		0	4
Merluccius productus			2	2
Cololabis saira	3	4	7	53
Atherinops affinis			6	0
Sebastes sp.			13	3
Perciformes			2	2
unidentified and other fish	30	46	9	7
all fish	80	82	65	89
sea lion placenta	0	4	15	1
garbage and offal	7		13	3
other	0	5	0	2

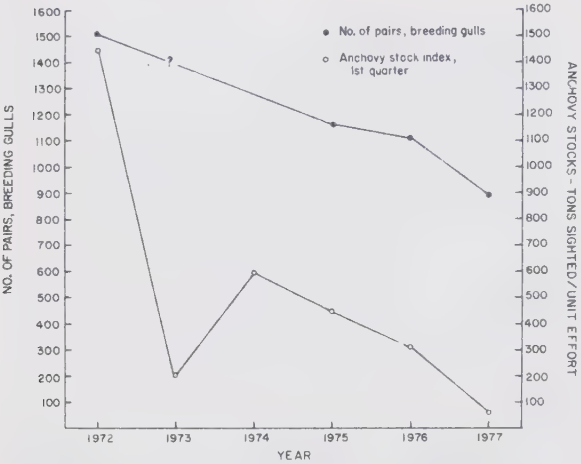

Figure 1. Recent changes in the number of Western Gulls breeding on Santa Barbara Island showing similar changes in the abundance of northern anchovies (see text for an explanation of the Anchovy Stock Index).

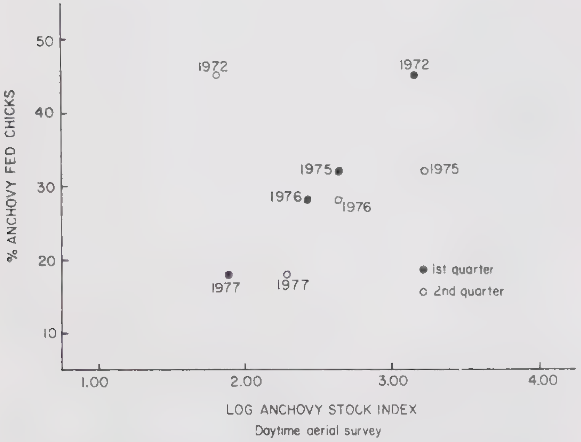

Figure 2. Relationship between the Anchovy Stock Index in the first quarter (January-March) and the second quarter (April-June) and the percent anchovies in the diets of Western Gull chicks.

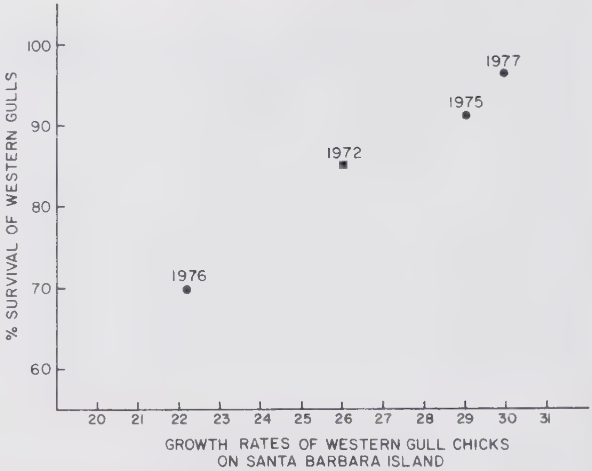

Figure 3. Relationship of Western Gull chick survival to their growth rates on Santa Barbara Island.

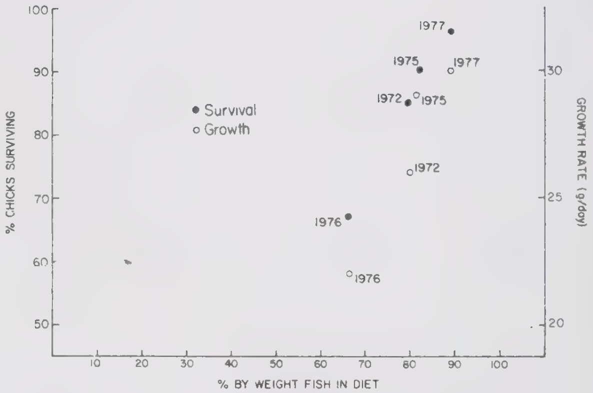

Figure 4. Relationship between the amount of fish in the diet fed young Western Gulls by adults and the growth and survival of gull chicks on Santa Barbara Island.

studies (Hunt and Hunt 1975, 1976a). Growth rates in turn were influenced by the amount of fish in the diets of chicks (Figure 4; $r = 0.98$, $N = 4$), but they were not significantly correlated with the percent of anchovies in the diet ($r = 0.30$, $N = 4$). In 1977 growth rates were high, despite the reduced use of anchovies. The use of sauries clearly made up for the lack of anchovies in 1977.

The timing of egg laying by Western Gulls might have also been expected to be sensitive to food availability (Hunt and Hunt 1976a). However, on Santa Barbara Island there was virtually no difference in the mean date of egg laying for any of the four years studied (Figure 5).

In contrast, Xantus' Murrelet clutch initiation varied in 1976, 1977, and 1978 (Figure 6). In 1978, murrelet egg laying was delayed by five to six weeks. When laying did begin, the number of birds nesting appeared reduced. Additionally, the interval between laying of eggs and the period of time between exchange of incubating adults was increased (Hunt et al. 1979).

Murrelets eat larval fish, particularly larval anchovies (Hunt et al. 1979). According to Lasker (1979), in 1978 larval anchovies failed to survive the stage of first feeding until after March. Thus, the late-larvae of the anchovies, upon which these birds appear to be specialized foragers, would not have been available until late April or early May, instead of in late February or early March as is more usual.

DISCUSSION

This study shows that Western Gulls feed their chicks a wide variety of foods, most of which are pelagic in origin

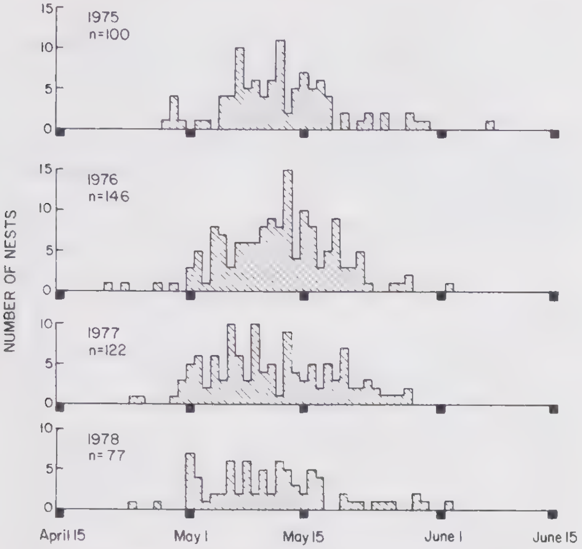

Figure 5. Clutch initiation in Western Gulls, Santa Barbara Island.

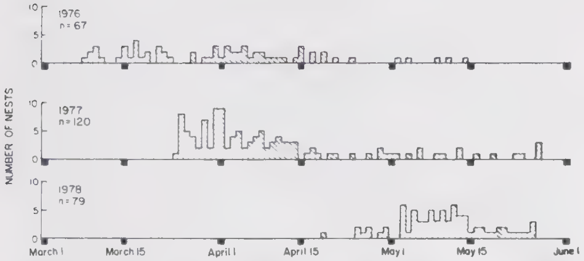

Figure 6. Clutch initiation in Xantus' Murrelets, Santa Barbara Island.

and few of which can be considered offal. Each colony tends to differ from other colonies in the kinds of foods taken, and these variations are believed to reflect relative availability of foods.

Hunt and Hunt (1975) concluded that the reproductive success of this population of Western Gulls was clearly related to the availability of anchovies. Daily fluctuations in the delivery of food to the chicks in 1972 were correlated with the percent of anchovies brought to Western Gull chicks. The present study also suggests the importance of anchovies to the Western Gulls of Santa Barbara Island. However, we now find that Western Gulls can make use of alternative foods and have nearly as good reproductive success. Early in the breeding season, anchovy availability may determine the number of gulls attempting to breed. Later, during the chick phase, the presence of abundant, nutritious pelagic forage fish, regardless of species, appears critical. When gulls turned to distant, less nutritious (Hunt 1972) garbage (Table 4, 1976), growth rates and reproductive success declined.

As additional data on anchovy abundance become available, it will be interesting to see if the number of gulls attempting to breed at Santa Barbara continues to track changes in anchovy populations. There appears to be uncertainty about the true size and health of the central stock of northern anchovies in the California Current. The numbers of breeding gulls at Santa Barbara Island may provide an index of their prey populations, much as have the guanay birds in Peru and southern Africa (Crawford and Shelton 1978; Murphy 1973; Jordan 1967).

The contrast between the reaction of the gull population and the murrelet population to food shortage is remarkable. In particular, the murrelets apparently delay reproduction while food is scarce. The Xantus' Murrelet has one of the largest eggs and clutches in relation to adult body weight of any seabird (Sealy 1975). This species may have a very precarious energy balance when it comes to egg production and may have no option but to delay egg-laying if its preferred foods are scarce. The delay in breeding in 1978, coupled with the greater interval between laying of eggs and incubation exchange, supports this hypothesis.

In contrast, the Western Gull showed no striking changes in the date of egg laying. For this species the ratio of egg weight or clutch weight to female body size is relatively small, and with the addition of courtship feeding by the male (Hunt in press), the female may not be under particularly strong energetic constraints. However, because Western Gulls nest in the open, unlike murrelets which nest in caves or under bushes, and because chicks are sensitive to thermal stress (Hunt et al. 1979; Bennett, unpublished field notes; Sayce, unpublished field notes) delay of gull reproduction may increase exposure of chicks to lethal thermal stress. Thus, Western Gulls that are unable to procure sufficient energy for egg production at the appropriate season may forego reproductive effort entirely for that season. The low chance for survival of chicks hatched late in the season would not compensate for the effort and risk expended in attempting to reproduce. Rather, these birds stay in the vicinity of the colony, but do not attempt to hold territory or lay eggs.

These differences in the reaction of two species of seabirds to apparent shortage of food provide a means of determining more precisely changes taking place in forage fish populations. Since the birds depend upon different life-history stages of the fish, changes in bird reproduction can be related to specific aspects of the fish populations and can be separated from effects due to weather, disturbance, etc. Thus, these seabirds provide a powerful, alternative tool for monitoring marine populations.

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The Feeding Behavior and Ecology of Marine Fish Larvae

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The behavioral-ecological traits of pelagic marine fish larvae diagnostic of specific ecological roles are discussed. Topics considered include: parental effects (egg size, yolk quantity, spawn distribution); swimming behavior; feeding and searching behavior; prey size relationships; and abundance and distribution of prey. Pertinent literature is reviewed and unpublished data on the larvae of northern anchovy, *Engraulis mordax,* and Pacific mackerel, *Scomber japonicus,* are presented. These two species are used as examples of two distinctly different ecological roles exhibited by marine fish larvae.

Introduction

Natural fluctuations in the size of fish populations are caused primarily by annual variability in the strength of incoming year classes. These may vary from about 0.3 to 2.0 orders of magnitude and this variability often has no obvious relation to size of parent stock (Cushing 1977).

Lack of understanding of the relation between stock and recruitment has hindered effective management of marine fish stocks. The loss in production from collapse of fisheries over the years has been huge. Murphy (1977) estimated a loss in production of clupeoid fishes of 600 million tons not including recent declines in Peruvian anchovy production. Many of these declines in production may be attributable in part to overfishing due to the failure of existing models to provide adequate management guidance owing to lack of understanding of recruitment. Many experts believe that studies of mortality in early life history stages, particularly that of eggs and larvae, hold the key to understanding the stock and recruitment relation (Hunter 1976a). Principal sources of larval mortality are generally believed to be starvation and predation. Thus, studies of behavior and ecology of larval stages in relation to these sources of mortality and stock size may provide much of the needed information. Aquaculture of marine fishes also depends upon adequate knowledge of the behavior of early life stages, for it is these stages that produce greatest technical difficulty in culture and highest labor costs. The objective of my report is to discuss behavioral-ecological traits of pelagic marine fish larvae that are diagnostic of specific ecological roles, and to consider such roles in relation to causes of mortality.

Parental Effects

EGG SIZE-YOLK QUANTITY-STARVATION

The size of a larva at the time of first feeding and the amount of time available to find food before onset of irreversible starvation are largely determined by the maternal influence of egg size and by water temperature. Shirota (1970) found that the length in mm of 40 species of marine and freshwater larvae at onset of feeding was related to egg diameter in mm by the simple relationship $L=4D$. Large size at onset of feeding is an advantage because larger larvae are able to swim faster and search a greater volume of water for food.

Larvae from large eggs generally have more time to find food before the onset of irreversible starvation because yolk persists for a longer period after feeding begins and/or the larvae have greater reserves in their body which can be used in metabolism (Blaxter and Hempel 1963). Larvae from small pelagic eggs are capable of existing for about 1-2 days after yolk absorption before onset of irreversible starvation, whereas larvae from large eggs such as herring and plaice are able to exist for 6 days and in grunion larvae starvation is reversible after 16 days (May 1971; Table 1). The ability to withstand starvation increases steadily from this point. At the beginning of metamorphosis, herring can withstand 15 days, plaice 23 days (Blaxter and Ehrlich 1974), anchovy 14 days, and Pacific mackerel larvae 5 days (Hunter 1976b and Hunter and Kimbrell MS). These differences reflect in part differences in activity; plaice are less active than herring at this time (Blaxter and Ehrlich 1974), and anchovy less than mackerel. Differences between older fishes reared in the laboratory must be considered only in a relative sense because of the striking differences in condition between reared and wild animals (Blaxter 1975).

TABLE 1. Vulnerability to starvation of eight marine fish larvae at the time of first feeding.

Species	Temp. °C	Size at hatch		yolk absorption	Days to point of no return[a] relative to:			Authors
		Length mm	Dry weight mg	Period (days)	Hatch	Yolk absorption	Onset of feeding	
Grunion *Leuresthes tenuis*	20	9.0	362	4	12+[b]	8+[b]	12+[b]	May (1971)
Clyde herring *(Clupea harengus*	7-8	8.2	189	8	25	6	22	Blaxter and Hempel (1963); Blaxter and Ehrlich (1974)
Haddock *Melanogrammus aeglefinus*	7	3.5	—	6-7	6	0-1	—	Laurence (1974); Laurence and Rogers (1976)
Pacific mackerel *Scomber japonicus*	19	3.1	40	3	4.0	1.0	1.6	Hunter and Kimbrell (MS)
Northern anchovy *Engraulis mordax*	16.5	2.9	21	4	7.7	1.5	2.5	Lasker et al. (1970); Hunter (unpubl. data)
Bay anchovy *Anchoa mitchilli*	24	2.5	18	1.7	3.1	1:4	1.7	Houde (1974)
Sea bream *Archosargus rhomboidalis*	22	2.3	28	2.2	3.4	1.2	1.7	
Lined sole *Archirus lineatus*	24	1.9	22	3.3	3.8	0.5	1.3	

[a] Time of irreversible starvation (Blaxter and Hempel 1963).
[b] 50% mortality from starvation, not a point of no return, because all survivors able to survive if fed.

The duration of egg incubation, although strongly affected by temperature, is also influenced by egg size. Ware (1975) found the relationship between the incubation time *(I)* at the water temperature for peak spawning, and egg diameter *(D)* for 14 species of Northwest Atlantic fishes was $D = 0.101\,I + 0.67$. Similarly, the duration of the yolk sac stage is also affected by egg size (Blaxter and Hempel 1963). Thus, larger eggs improve the survival capabilities of a larva at the onset of feeding, but at the cost of decreasing fecundity and increasing the duration of stages most vulnerable to predation.

The optimum egg size must strike a balance between numbers and the risks of starvation and predation. At lower temperatures where incubation periods are longer, the advantage generally falls to larger eggs, whereas the reverse appears to be true at higher temperatures (Ware 1975). Fine adjustments in these tactics appear to exist within a species to meet seasonal and regional differences in environment. Egg size varies significantly among spawning groups of herring (Blaxter and Hempel 1963) and is known to vary seasonally in many species, with the largest eggs produced in the spring at the coolest temperatures and egg size declining as the season progresses (Bagenal 1971; Ware 1975).

The estimation of the days to irreversible starvation has generally been made from the time of complete yolk absorption but the time from onset of feeding provides more insight to survival strategy, as most larvae begin to feed before the yolk is completely exhausted. Herring larvae have a prolonged period in which they are capable of feeding but still have yolk (Table 1). Thermal optima in efficiency of yolk utilization is another way larvae may adapt to specific environmental conditions. Sea bream larvae retain more yolk at the onset of feeding at 26°C than at other temperatures and thus have more yolk to sustain them if food is not present (Houde 1974). Plaice larvae have a sharply defined thermal optimum in yolk utilization efficiency between 6.5-8°C, which could produce 10% larger larvae at the time of first feeding (Ryland and Nichols 1967).

SPAWNING TACTICS

Eggs of pelagic spawners are often distributed in extremely patchy patterns; 37% of Pacific sardine eggs taken in the years 1951-1959 occurred in only 0.6% of the samples (Smith 1973). Helfrich and Allen (1975) found the density of mullet eggs *Crenimugil crenilabis* to be 17/L at the surface after about 1-2 sec of intensive spawning. A high density of northern anchovy eggs taken in a neuston net was 31/L, corresponding to a density of 46,000 eggs/10 m^2 of sea surface, which is in the upper 5% of all samples of anchovy eggs collected with nylon nets (unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). Other high egg densities include 31,000 eggs/10 m^2 for Pacific sardine (Smith 1973) and 9,000 eggs/10 m^2 for Atlantic mackerel (Sette 1943). The eggs in such patches gradually disperse; dispersion is more rapid at the perimeter of the patch resulting in a denser centrum surrounded by a less concentrated corona. The horizontal mean distance between neighboring eggs increases in a patch from 1-2 cm at spawning to 15-20 cm in most several-day-old sardine eggs (Smith 1973). In the northern anchovy, dispersion of larvae as measured by the negative binomial *K* (Lloyd 1967) continues from hatching until the larvae reach about 10 mm, at which time they reach their most dispersed state and contagion increases thereafter (J. Zweifel, unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). This change from decreasing to increasing contagion coincides with the time anchovies begin nightly migrations to the sea surface to fill their swim bladders (Hunter and Sanchez 1976) and is close to the onset of schooling which begins at about 12 mm by concentrating larvae near the surface at night and thus increasing the frequency of social contacts.

Dispersion of larvae could progress to the point where it might influence onset of schooling or delay formation of schools of viable size. *Menidia* larvae reared in isolation took more time to form a school when brought together than socially reared larvae and the length of the delay was proportional to the period of isolation (Shaw 1961). Breder and Halpern (1946) showed that *Brachydanio rerio* larvae reared from the egg in isolation had considerable hesitancy to join a school. Thus, onset of schooling could be retarded if larvae are dispersed to the point where social contacts are infrequent.

Intraspecific competition and cannibalism also may be affected by initial spawn density and dispersion rates. Houde (1975) found that growth and survival of sea bream larvae decreased rapidly when stocking density exceeded 8 eggs/L at food levels of 1500-3000 microcopepods per liter. Food concentrations of 100/L did not sustain sea bream larvae except at 2 eggs/L stock densities. Bay anchovy larvae (*Anchoa mitchilli*) seem to be much less affected by stock density (Houde 1975, 1977). Sibling cannibalism is common in rearing larvae of large piscivorous fishes such as the scombroids (Mayo 1973) but is unreported and presumably rare in clupeoid fishes. Thus, larger and more active larvae seem to be more prone to cannibalism and competition for food and possibly better able to find schooling companions because of faster swimming speeds. Formation of dense patches of eggs and slow dispersion rates may favor clupeoid larvae, but lower egg densities may be more favorable to the more active larvae.

Swimming Behavior

The cruising speed of larvae is of major importance in their feeding ecology because it affects the frequency that larvae encounter prey, and also accounts for the greatest metabolic expenditure. Swimming of larvae may differ somewhat from adults due, in part, to the lack of mechanical support of the caudal fin. Tail beat amplitude and tail beat frequency are continuously modulated in northern anchovy larvae (Hunter 1972) and Pacific mackerel larvae (Hunter and Kimbrell, MS), whereas in adult fishes amplitude is modulated less frequently, except during accelerations (Hunter and Zweifel 1971). Tail beat frequency is inversely proportional to length in fishes (Bainbridge 1958; Hunter and Zweifel 1971), and consequently, the frequency in early larval stages can be quite high, reaching 50 beats/sec in 4- to 5-mm anchovy and Pacific mackerel larvae. At their cruising speed, anchovy larvae use a beat and glide mode of swimming similar to that of adults. This mode of swimming is slow and thereby reduces the volume of water that can be searched, but it has a high metabolic efficiency (25% in a 15-mm larva; Vlymen 1974).

Temperature can have a major effect on activity or cruising speed. Two effects of temperature on activity are illustrated for the northern anchovy reared to age 12 days at various temperatures on a diet of *Gymnodinium splendens* (Fig. 1). Temperature affected the timing of the transition from the inactive yolk-sac stage to the active feeding stage as well as having a direct effect on activity of older larvae. At age 4 days, negligible feeding activity occurred in larvae at 15°C or lower and the speed-temperature relation was a function of developmental rate. At ages 8-12 days, all larvae were past this transition and a direct effect of temperature on activity is evident in the figure.

Cruising speeds increase markedly over larval life more or less in proportion to length. Blaxter and Staines (1971) observed that the cruising speed of herring larvae increased from 20 cm/min at the end of yolk-sac stage to 80 cm/min 8 wk later; in pilchard *(Sardina pilchardus)* speed increased from 10 to 30 cm/min in 3 wk; in plaice from 10 to 60 cm/min over 7 wk; and in sole *(Solea solea),* from 5 to 40 cm/min over 7 wk. They also noted that cruising speeds of flatfish, sole and plaice dropped by 90% at metamorphosis. Similarly, oxygen consumption of winter flounder *Pseudopleuronectes americanus* was shown by Laurence (1975) to decline sharply at metamorphosis.

Specific comparisons in activity or swimming speed from the literature are difficult to make because of differences in temperature, methodology, and lack of data on larval size. Data collected in my laboratory on anchovy and mackerel show that anchovy larvae swim more slowly than mackerel larvae at all stages of development (Fig.

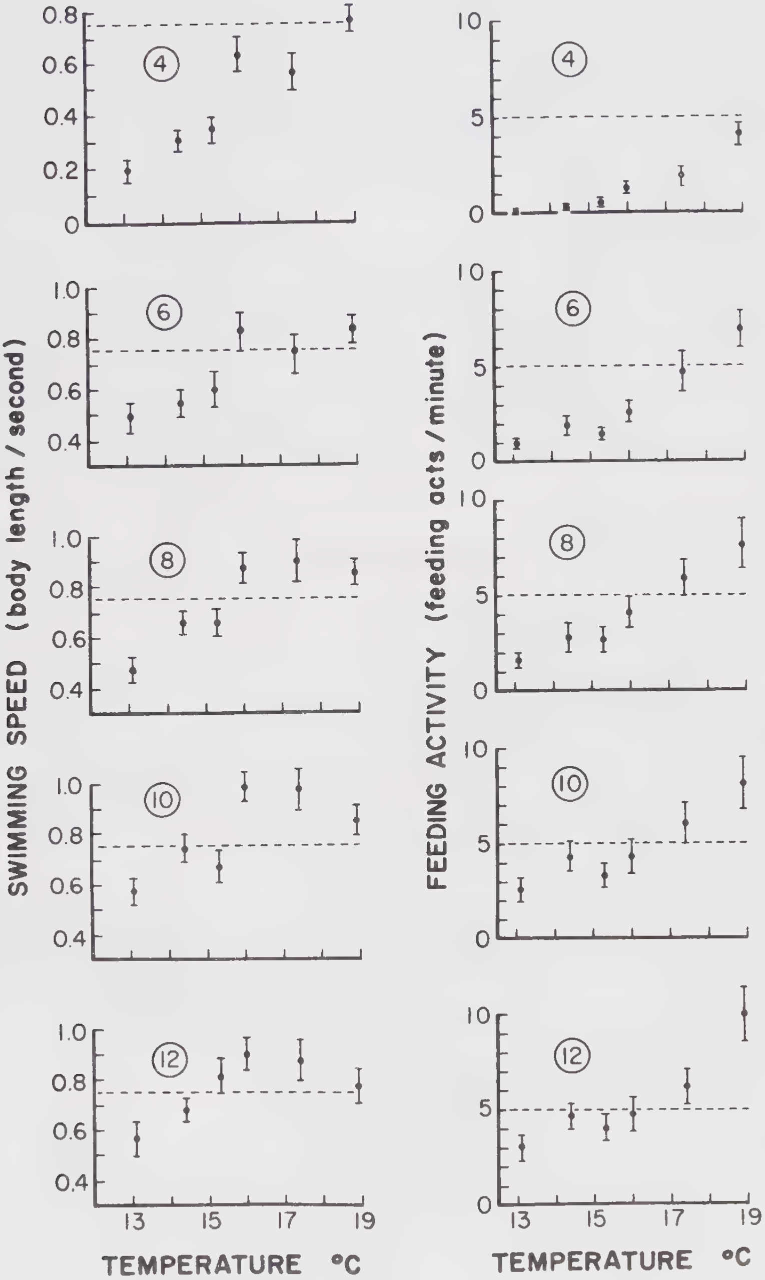

Fig. 1: Effect of temperature on swimming speed and feeding rate of northern anchovy fed *Gymnodinium splendens* (mean density 400 cells mL). Points are means, bars are 2x standard error of mean, panel numbers are larval age in days, and dashed line is a visual reference. Data based on direct visual observation of larvae for 5-mm intervals. Each point is average value for 15 fish in two or more rearing groups.

2). Such a striking specific difference in cruising speed is diagnostic of major differences in life history tactics because it implies marked differences in searching abilities and metabolic requirements. For example, at 18°C, anchovy larvae consume 4.5 μL 0_2. mg dry wt^{-1} h^{-1} whereas mackerel consume 6.1 μL 0_2 . mg dry wt^{-1} h^{-1} (Hunter 1972 and Hunter and Kimbrell MS). The actual difference in metabolic rate between these species is probably greater because the larvae were confined in small Warburg flasks which probably reduced the activity.

Blaxter (1969) concluded from his review that cruising speeds of larval fishes are on the order of 2-3 body lengths/sec and burst speeds, speeds that can be maintained for a few seconds, are on the order of 10 body lengths/sec. The cruising speed of the anchovy is close to 1 body length/sec and in mackerel it increases from 2 to 3 during the larval stage. Thus, these two speeds approach the upper and lower limits of the general range of cruising speeds.

Feeding Behavior

PREY PERCEPTION AND RECOGNITION

Marine fish larvae are visual feeders. All those studied so far, plaice, herring and anchovy, lack rods and retinomotor pigment migration during the first weeks or months of life (Blaxter 1968a, 1968b; C.O'Connell, pers. comm., National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). That feeding is confined to daylight hours is also indicated by stomach content analysis in other species (Arthur 1976).

To be perceived, a prey must be relatively near; first-feeding herring larvae react to prey at 0.7-1.0 body length (L) (Rosenthal and Hempel 1970) or 0.4L (Blaxter and Staines 1971); plaice at 0.5L and pilchard at 0.2L (Blaxter and Staines 1971). Ninety-five percent of the prey reacted to by northern anchovy were within 0.4L of the axis of progression (Hunter 1972).

It would be unreasonable to attach much importance to differences among these values between species. The factors controlling perceptive ranges in larval fishes have not been studied and size of prey was not isolated as a variable. In adult planktivorous fishes, perceptive distances appear to be a linear function of prey size (Confer and Blades 1975). If perceptive distances increase with prey size in larvae, this would certainly increase the effective searching volume of larvae specializing in such prey. In all these studies, the authors point out that perceptive ranges increase as larvae grow. Rosenthal and Hempel (1970) concluded that perceptive ranges in herring larvae also change with activity level, being greater during slow meandering swimming and shorter during faster swimming.

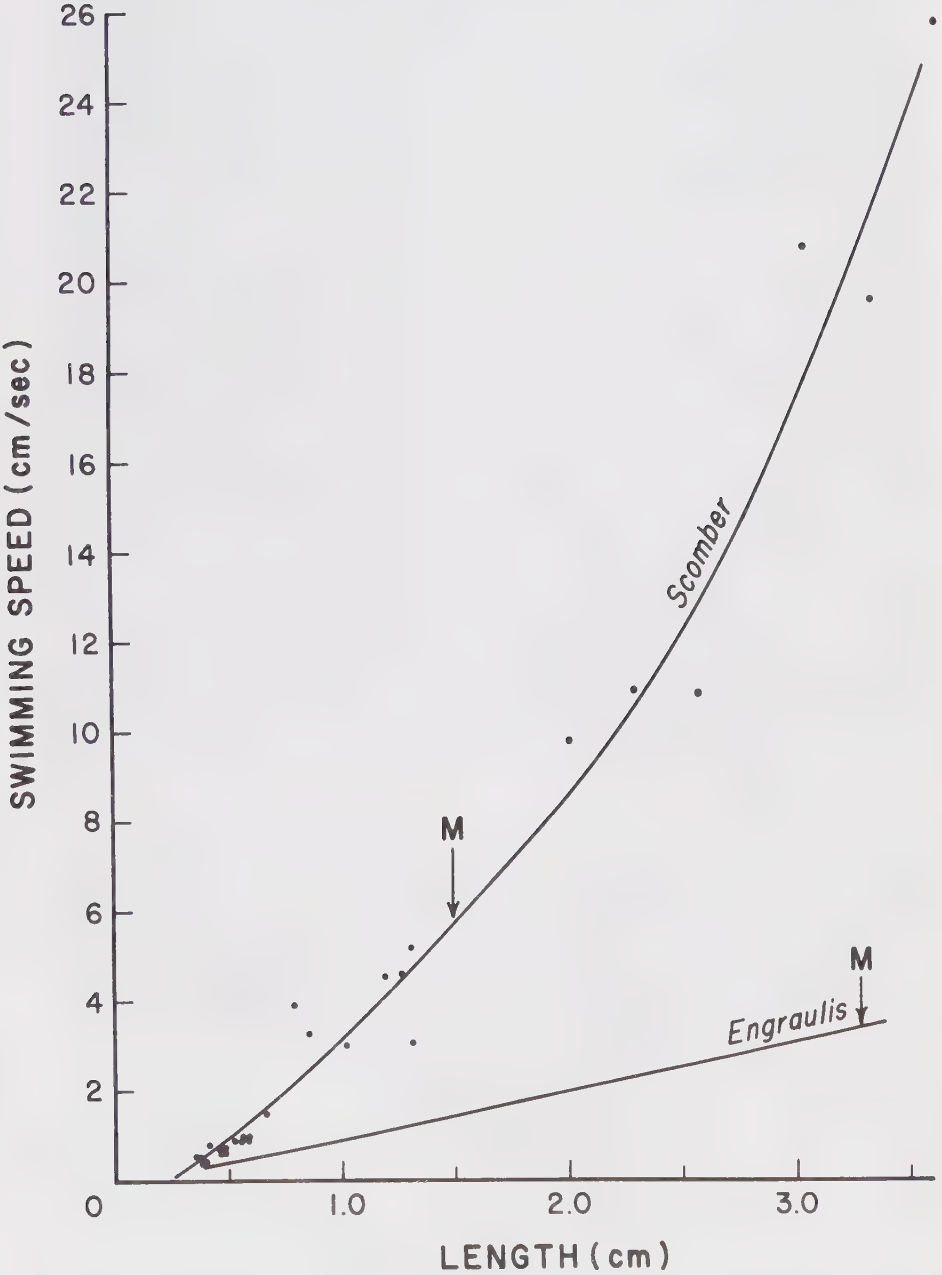

FIG. 2. Swimming speed of Pacific mackerel, *Scomber japonicus*, larvae and juveniles at 19°C; points are means for five or more observations; curve fit by eye; and swimming speed of northern anchovy larvae, *Engraulis mordax*, at 17-18°C from Hunter (1972). Speeds are total distance covered, including time spent in rest and feeding, and M indicates fish length at metamorphosis.

They also state that herring larvae do not perceive prey which are beneath the plane of the horizontal axis of the body, but this does not appear to be the case for northern anchovy larvae (Hunter 1972).

The stimuli eliciting prey capture have not been studied in larval fishes, but in adult fishes prey size is usually the strongest factor with movement seeming to direct attention of the fish toward the prey (Kislalioglu and Gibson 1976a). Almost all predators which are believed to depend upon prey movement are able to detect prey even when they are motionless (Curio 1976). The frequent occurrence of copepod eggs and other nonmotile foods in the stomachs of field-caught larvae and *Artemia* eggs and other nonmotile foods in laboratory-reared larvae (May 1970) clearly shows that movement is not essential in many species. Prey size selection so dominates selection patterns in larval fish that it is difficult to evaluate the role of other prey characteristics such as spines and other protective structures, color, or avoidance behavior. Bowers and Williamson (1951) concluded that some copepods with spiny appendages such as *Acartia* occurred in the stomachs of herring larvae less frequently than would be expected from their abundance in the plankton, and Arthur (1976) suggested that jack mackerel may select the more brightly colored copepods such as *Microsetella* which occur in their stomachs in greater abundance than in the plankton. It would be of considerable interest to study such characteristics under controlled laboratory conditions, both from the standpoint of larval feeding ecology and copepod evolution.

MOTOR PATTERNS

Upon sighting a prey clupeoid larvae assume a sinuous posture and advance toward the prey by sculling the pectoral fins and undulating the finfold while maintaining the body in the S-posture. When the prey is a short distance from the snout, the larva opens its mouth, straightens its body causing the body to drive forward, and the prey is engulfed (Breder and Krumholz 1943; Rosenthal and Hempel 1970; Hunter 1972). Larvae of plaice *Pleuronectes platessa* (Riley 1966) and northern sennet *Sphyraena borealis* (Houde 1972) and other fishes are also reported to assume a sinuous feeding posture but the behavior has been studied in detail only for clupeoids and for freshwater coregonid larvae *Coregonus wartmanni* (Braum 1964), and quite possibly differences exist among species.

Pacific mackerel larvae *Scomber japonicus* feed in a manner more typical of the biting attack of many adult fishes. Upon sighting a prey, mackerel larvae advance toward the prey, stop, draw back the tail, and hold it in a slightly recurved, high amplitude position. The rest of the body is straight; feeding is accomplished by opening the mouth and driving the tail posteriorly. Presumably many other larvae of similar robust body form feed in this way.

Anchovy larvae often assume and reassume the S-posture while maintaining their orientation to a moving prey; but my observations indicate that once the strike is made, larvae rarely strike again at the same prey. Mackerel larvae, on the other hand, frequently strike two or more times at the same prey if the previous strike was unsuccessful. Mackerel larvae often reposition for the second strike by moving backward; anchovies and other clupeoid fishes do not appear to have this maneuverability (Blaxter and Staines 1971). Large prey are more difficult to capture and are less abundant in the sea; consequently, persistence in a feeding attack as exhibited by mackerel may be an essential characteristic of a species whose strategy depends on larger prey.

The time spent poised in a striking posture is much longer at the time of first feeding than in later larval life, and gradually the strike becomes integrated with swimming movements. In the anchovy, duration of complete feeding acts declined from 1.5-2.0 sec to about 0.6 sec when larvae reached 17 mm and relative speed of the strike also declined (Hunter 1972). A poised striking posture seems to be a common tendency in young larvae and declines as the larva grows and could be an adaptation to low feeding success, and perhaps to a necessity to feed by engulfing prey that are relatively large for their mouth.

Handling times are negligible when copepods and other small zooplankton are prey because the prey are engulfed by the mouth instantaneously. Piscivorous fish larvae manipulate their prey and consequently handling times increase with prey size as is the case for adult fishes (Kislalioglu and Gibson 1976b). The appearance of piscivorous habits requires development of a new set of motor patterns associated with grasping prey and presence of sufficient numbers of teeth to accomplish this end. Larvae of the northern sennet *Sphyraena borealis* usually seize other larvae crosswise and, by a successive series of head shakes, move the grasp to either the head or tail. Then without losing grip, the prey is swallowed head or tail first (Houde 1972). Houde observed that newly hatched fish larvae were eaten by sennets at age 10 days and were the preferred food of sennets 9 mm and longer. I observed the same behavior in the Pacific barracuda *Sphyraena argentea* feeding on siblings in a rearing tank. In this case, piscivorous feeding began at age 5 days when larvae were only 4.4 mm. Pacific mackerel larvae become piscivorous when they reach 10 mm. They also seize other larvae from the side, carry them crosswise in the mouth, periodically release the prey, and grasp it again until it dies; then they release it and ingest it, usually head first.

FEEDING SUCCESS

Feeding success of fish larvae is often low at the onset of feeding. Estimates for herring are 6% (Rosenthal and Hempel 1970) and 2-6% (Blaxter and Staines 1971), for coregonid larvae 3-5% (Braum

1964), and 10% for northern anchovy (Hunter 1972). Feeding success gradually increases, reaching 90% in about 3 wk in the anchovy (Hunter 1972), and in about 7 wk in herring (Blaxter and Staines 1971). In contrast to these species, plaice larvae capture 32-62% of prey attacked at the onset of feeding (Blaxter and Staines 1971) and the relatively large larvae of *Belone belone* (12 mm) capture 60-100%, depending on prey type (Rosenthal and Fonds 1973).

Blaxter and Staines (1971) suggest that the initially high success of plaice larvae may be due to increased maneuverability of plaice relative to herring and to their ability to swim backwards. Feeding success of anchovy larvae dropped from 80% to 40% at age 17 days when the prey was changed from *Brachionus* to *Artemia* nauplii, but in 2 days their success increased to the former level (Hunter 1972). Changes in mouth size or other developmental changes could not occur so rapidly; thus, the difference appears to be attributable to experience.

SEARCHING BEHAVIOR

Food density requirements have been estimated from behavioral search models of the basic form outlined by Ivlev (1960). These models in their simplest form require an estimate of ration, swimming speed, perceptive field, and feeding success with many other parameters added as complexity increases. These models range in complexity from the simple models of Rosenthal and Hempel (1970), Blaxter and Staines (1971) and Hunter (1972) where only basic parameters are considered, to the increasingly complex models of Jones and Hall (1974) and the most complex to date, Vlymen (1977). Vlymen's model is the only one that does not assume a random search pattern and that addresses the problem of a contagious food distribution. In his model the larvae have no effect on food density and the model does not use a prey size dependent modulation of perceptive field and feeding success. All such models are extremely sensitive to assumptions regarding the perceptive field and swimming speed and to the accuracy of these measurements. For example, Blaxter and Staines (1971) estimated that the searching abilities of herring larvae increased from 0.1 to 2.4 L/h over 8 wk, whereas Rosenthal and Hempel (1970) estimated they increased from 1.5 L to about 10 L/h in 10 wk. The major difference in these results is in the differences in perceptive distances and rates of swimming (Blaxter and Staines 1971). It would seem to be of value to use such models to set up hypotheses that could be tested in the laboratory or at sea.

Owing to these problems and to effects of temperature, specific comparisons are difficult but these estimates do suggest that the volume searched by young larvae is often quite small: pilchard (5-7 mm) search 0.1-0.2 L/h, plaice (6-10 mm) search 0.1-1.8 L/h

(Blaxter and Staines 1971) and anchovy (6-10 mm) search 0.1-1.0 L/h (Hunter 1972). All studies show that searching abilities increase markedly with growth, since speed, capture success rates, and perceptive distances are functions of length or age.

In the two cases studied, search patterns in larval fishes were non-random. Larval anchovies decrease their speed and change their turning probabilities when they enter a dense patch of food. The probability of making a complete reversal in direction increased from 0.04-0.05 at low food densities to 0.23 in dense patches of *Gymnodinium* and to 0.07 in patches of *Brachionus* (Hunter and Thomas 1974). Wyatt (1972) showed that the time plaice spent swimming increased with a decrease in food density. Similar non-random search patterns have been described for adult fishes (Kleerekoper et al. 1970; Beukema 1968).

Prey Types

Naupliar through adult stages of copepods are the typical food of most marine fish larvae studied to date. Some notable exceptions to this rule exist: in the North Sea in normal years, the food of plaice larvae consists mostly of the appendicularian *Oikopleura dioica* (Shelbourne 1962) and larval fishes may be a common item in the diet of the more piscivorous larvae. Larvae are commonly eaten by larval Pacific barracuda (A. Ahlstrom, pers. comm., National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA) and blue marlin *Makaira nigricans* (Gorbunova and Lipskaya 1975), and judging by high incidences of cannibalism under rearing conditions, they may be frequently eaten by many scombroid larvae (Mayo 1973). Blue marlin larvae begin feeding on fish larvae at 6 mm and they become the principal food by 12 mm (Gorbunova and Lipskaya 1975); under rearing conditions, the scombroid fishes, *Euthynnus alletteratus, Scomberomorus cavalla, Scomberomorus regalis* and *Auxis* became cannibalistic at about 5 mm (Mayo 1973), *Scomber japonicus* at 10 mm, and *Sphyraena argentea* at 4.4 mm (Hunter, unpublished data). Under aquarium conditions, sibling cannibalism appears to end as scombroid fishes become juveniles and begin schooling (Mayo 1973; Clemens 1956; Hunter and Kimbrell MS).

Larvae tend to be more euryphagous during the earliest stages and organisms such as tintinnids, phytoplankton, mollusk larvae and ciliates are often eaten as well as copepods (Arthur 1976; Bowers and Williamson 1951; Lebour 1921; R. de Mendiola 1974). Phytoplankton, often identified as green remains, is relatively common in the stomachs of clupeoid larvae at about the time of first feeding, but is uncommon soon after. In general, the use of phytoplankton in laboratory rearing studies as a sole source of food for first-feeding larvae has been unsuccessful (May 1970). Northern anchovies, on the other hand, are able to subsist on a diet of the dinoflagellate *Gymnodinium splendens* for up to 20 days, but at a greatly depressed growth rate (Lasker et al. 1970; Theilacker and McMaster 1971). Anchovies will feed on a variety of dinoflagellates, *Gymnodinium, Gonyaulax, Prorocentrum* and *Peridinium,* but not small flagellates, *Chlamydomonas, Dunaliella,* nor on diatoms, *Ditylum, Chaetoceros, Thalassiosira* and *Leptocylindrus* (Scura and Jerde 1977). That larvae fed *Gonyaulax* (40 μm diameter) did not survive, whereas those fed *Gymnodinium* (50 μm diameter) did, led Scura and Jerde to conclude that it was the small size of *Gonyaulax* which made it an inadequate food. Using the same line of reasoning, it seems doubtful that any of the other dinoflagellates they studied would support growth because they are even smaller in diameter.

The tendency for larvae to feed upon a greater variety of organisms in early larval life and subsequent specialization in stages of copepods may simply be due to the existence of a greater variety of small organisms of the proper size in the sea. The ability to subsist on the relatively small organisms such as dinoflagellates may be restricted to larvae of relatively modest energy demand, such as the northern anchovy, i.e., a larva of relatively low initial weight, low activity, existing in cool water.

Prey Size Relations

Specific Differences

Size dominates prey selection patterns of larval fishes and is one of the best diagnostic characteristics for evaluating specific ecological roles. The critical dimension for ingestion of copepods and other oblong prey is the maximum width including appendages (Blaxter 1965; Arthur 1976). Evidence for this is based on the fact that copepods are frequently found in the stomachs of larval fishes which were too large to be ingested in any other way (Blaxter 1965; Hunter 1977). Copepods are usually found in the stomachs of clupeoid larvae with antennae folded back along the body (Blaxter 1965). Blaxter goes on to say that copepods with antennae folded in such a way are probably the only ones that are captured successfully. Inclusion of the appendages increases the maximum width of adult and copepodite stages by about 49% in *Pareuchaeta,* 25% in *Calanus, Pseudocalanus, Acartia, Microcalanus,* and *Metridia,* but has a negligible effect in *Temora, Oithona, Oncaea,* and *Microsetella* (Wiborg 1948a).

The increase in size of prey selected by marine fish larvae as they grow is well documented in the literature and occurs in every species studied. Often, prey length or life stage was used as a measure of size rather than the more informative measurement of maximum prey width. A striking feature of these data is the consistency of trends among related species and groups (Fig. 3). The small clupeoid larvae, *Sardinops, Engraulis,* and *Harengula,* consistently feed on small prey of the order of 50-200 μm width; both species of *Trachurus* show a tendency for a marked increase in the range of food sizes eaten with length; and *Scomber* shows a somewhat similar trend. In the three engraulid species, there appears to be a consistent tendency for a marked increase in the range of prey eaten between 8 and 12 mm. Hake larvae begin feeding on much larger foods than the rest with only a slow increase in average prey size. De Ciemchomski and Weiss (1974) point out that hake begin feeding on advanced copepodite and adult stages of copepods.

The consistency of these trends from different localities and species strongly suggests that these patterns are the result of positive size selection inherent to species or specific ecological groups of larvae. Stepien (1976) demonstrated that sea bream larvae select foods by size, with a slight positive electivity for prey of 100-200 μm width in larvae 4-5 mm and a stronger positive electivity for prey 200-300 μm in larvae 7-9 mm. The difference between sea bream and the two clupeoid larvae in the figure may be more marked under natural conditions because the food size preference of sea bream increased faster than the increase in size of the food in the rearing tanks.

Except for hake, specific differences are less marked at the onset of feeding with all larvae feeding on prey of 50-100 μm width although jack mackerel take much larger foods as well. Houde (1973) remarks that organisms 50-100 μm are eaten by a great variety of larvae at this time, including those with relatively large mouths such as the tunas and flatfishes. Arthur (1977) estimated the naupliar biomass in the California Current system and expressed it in terms of naupliar width. The naupliar biomass was at a maximum between 50-80 μm of naupliar width and declined sharply on either side even though there were many more nauplii of smaller sizes. He points out that the food size range of first-feeding Pacific sardines, northern anchovies and jack mackerel all overlap the naupliar biomass maximum and it appears that the feeding range of many other larvae do so as well.

Larvae in the above comparisons are relatively the same size at onset of feeding and hatch from relatively small eggs. Larvae from large eggs, for example, exocetid larvae and saury *Cololabis saira* are 6-7 mm at first feeding and feed on a range of prey equivalent to that of older jack mackerel or *Scomber* of about the same size (Yokota et al. 1961). None of the species in Fig. 3, other than hake, could eat newly hatched *Artemia* nauplii at the onset of feeding, but rearing studies reviewed by May (1970) indicate that plaice larvae, two species of *Fundulus,* a species of *Sebastes,* two cottid species, four species of atherinids, *Aulorhynchus flavidus,* and *Fugu pardalis*

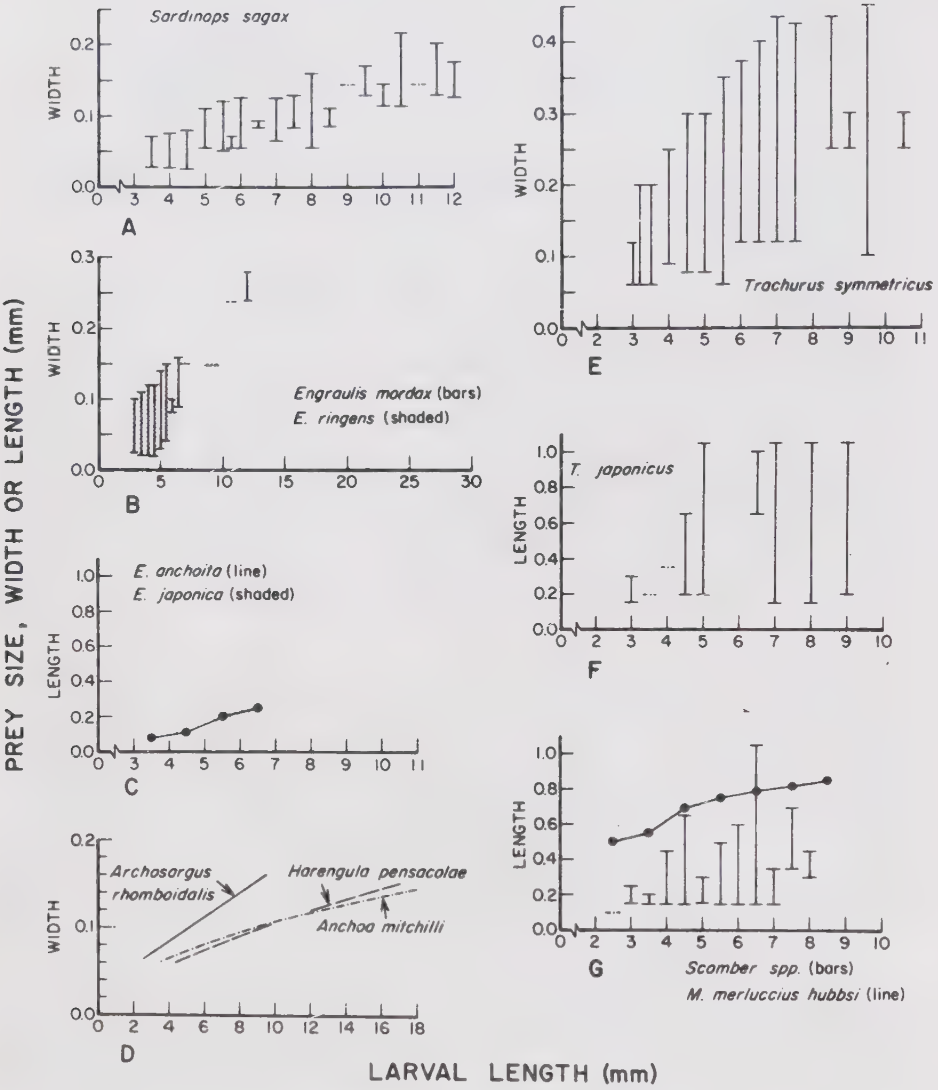

FIG. 3: Relation between prey size and larval length for 12 species of marine fishes; label on ordinate indicates if prey width or prey length were measured; vertical bars and shaded areas represent range of prey sizes; and straight lines connecting dots indicate average prey sizes. Plots were redrawn from Arthur (1976) for *Sardinops sagax, Engraulis mordax* and *Trachurus symmetricus;* from R. de Mendiola (1974) for *Engraulis ringens;* from Detwyler and Houde (1970) for *Harengula pensacolae* and *Anchoa mitchilli*; from Stepien (1976) for *Archosargus rhomboidalis*; from Cieschomski and Weiss (1974) fro *Engraulis anchoita* and *Merluccius merluccius;* and from Yokota et al. (1961) for *Engraulis japonica, Trachurus japonicus* and *Scomber* spp. Data are for sea-caught larvae, except panel D which were laboratory reared.

feed successfully on *Artemia* nauplii at the onset of feeding. Many of these species have large eggs, again emphasizing the importance of the maternal contribution in the feeding tactics of some larvae.

An additional feature of importance in these records is the slow increase in the minimum size of prey eaten in all species. The effect of this is to greatly expand the prey range in larvae that select larger prey. In summary, marine larvae select foods of increasingly larger size as they grow, but the average and range of sizes selected differ greatly among species and may be diagnostic of specific ecological roles.

Effect of Mouth Size

The size of the mouth and the rate it changes with length must be partially responsible for specific differences in food size selection. Shirota (1970) measured the gape of the mouth of 33 species of marine and freshwater larval fishes, correlated them with the size of natural foods and growth rates, and concluded that larvae with smaller mouths grew more slowly than those with larger ones. Blaxter (1965) showed that differences in gape of the mouth existed between different races of herring, and concluded that these differences could be of great significance in early survival.

Mouth size would be expected to set the upper size limit for prey. To define this relationship, Hunter (1977) and Hunter and Kimbrell (MS) determined for anchovy and Pacific mackerel the mouth size threshold for various prey. In these experiments, larvae were exposed to high densities of a single prey, *Brachionus, Artemia* nauplii, or anchovy eggs, for 2-4 h and the proportion of larvae that captured one or more prey was tabulated by mouth size classes. None of the larvae tested had any previous experience with the particular prey. The width of the mouth was closely correlated with the ability to capture these prey (Fig. 4). The first incidence of feeding occurred when the ratio of prey width to mouth width was close to unity, when *Artemia* or anchovy eggs were the prey. In the case of *Brachionus*, it was lower (0.63) which may have been caused by the fact that first-feeding anchovy larvae were used in this experiment to avoid the effect of rapid improvement of success that occurs over the first few days.

These experiments indicated that on the average, 50% of larval anchovy or mackerel were capable of feeding on these prey when the prey width to mouth width ratio was 0.76. The width of the mouth provided a good indication of the size of prey a larva was capable of ingesting. Mouth gape was also measured but width was preferred because it could be measured with greater accuracy. A different relation could be expected for piscivorous feeding or when ingestion involved manipulation of the prey because larvae are capable of greatly expanding their mouths under these circumstances. The

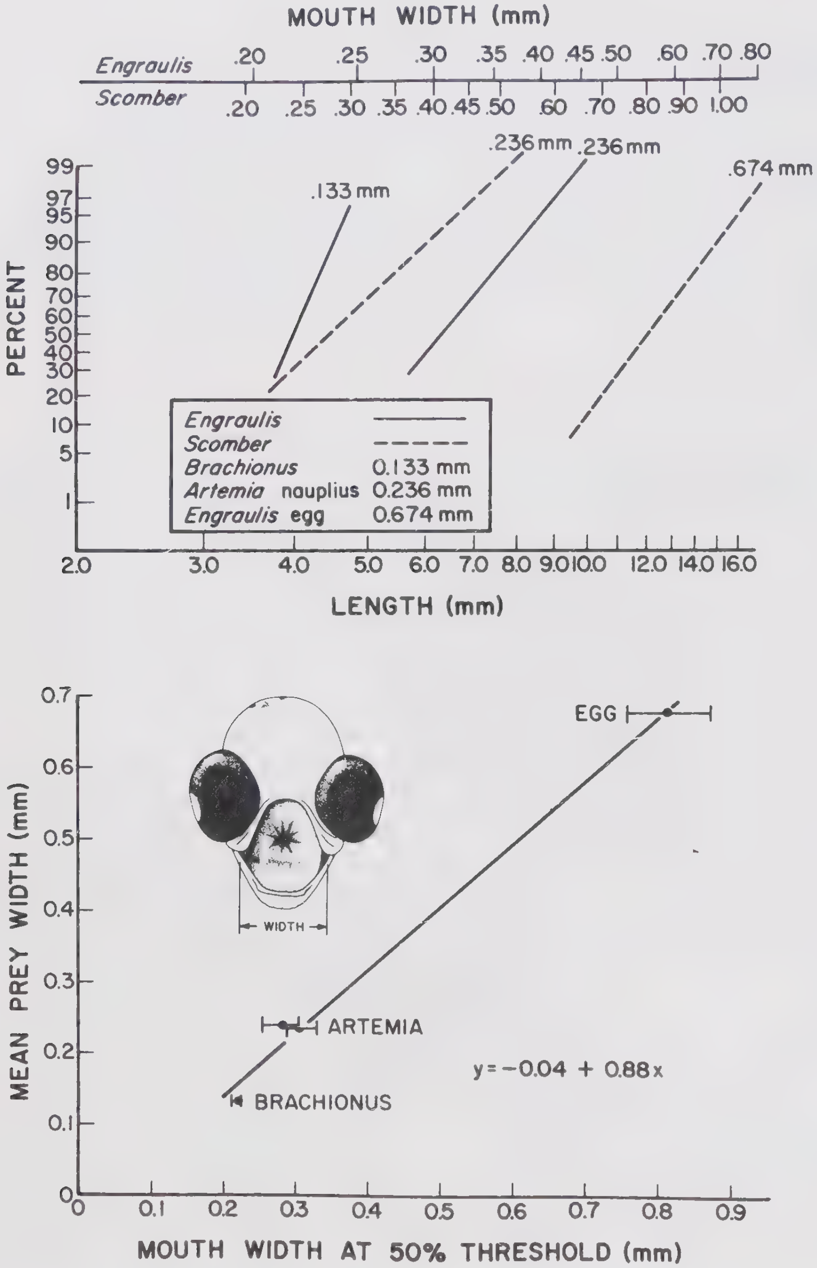

FIG. 4. Relation between width of mouth and ability of *Scomber japonicus* and *Engraulis mordax* to capture prey of various widths. Upper panel, percent of larvae that captured one or more prey shown as a function of mouth width (upper scales) and larval strength (lower scale); lines are for the regression of probit on log larval length. Lower panel, average width of prey shown as a function of the mouth width at which 50% of the larvae ingested one or more prey; estimates taken from probit lines given in upper panel; and bars are the 95% confidence intervals for the estimate. Density of prey in the experiments were: *Brachionus* 9/mL; *Artemia* 10/mL; and *Engraulis* eggs 10/L.

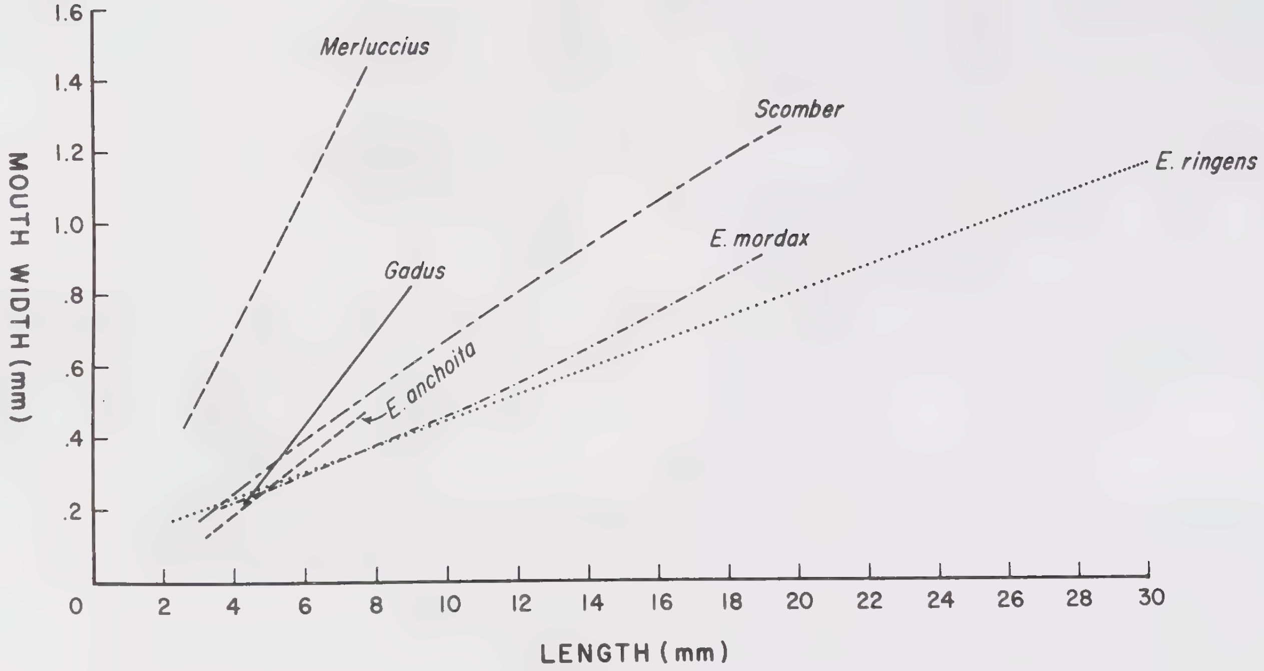

Fig. 5. The relation between mouth width and larval length of hake, *Merluccius merluccius* from de Ciechomski and Weiss (1974); cod, *Gadus morhua* from Wiborg (1948b); Pacific mackerel *(Scomber japonicus)* from Hunter and Kimbrell (MS); and three species of anchovy, *Engraulis anchoita* from de Ciechomski and Weiss (1974). *Engraulis mordax* from Hunter (1977) and *Engraulis ringens* from R. de Mendiola (1974).

gape of the mouth would be expected to be related to handling time in this case (Kislalioglu and Gibson 1976b).

These thresholds are also of interest because they indicate how feeding success is affected by prey size. They also show that prey are eaten "end first" because at the lowest success levels, the prey could be ingested in no other way. Many of the trends in size selection of prey discussed in the previous section are also suggested by the relationship between mouth width and length. The mouth sizes of the three engraulid species are similar to each other and differ markedly from those of the other species (Fig. 5). The mouth width of all species but hake are somewhat similar in the beginning but differences increase greatly with growth. Hake stand out as being distinctly different from the rest from the onset of feeding.

The sharp increase in food size that occurs in the engraulids between 8-12 mm occurs at a time anchovies become highly proficient in capturing *Artemia* nauplii and the increase in prey size is to one of that diameter. No evidence exists from mouth size information to explain the leveling of food size that occurs thereafter, despite the fact that the mouth continues to grow. It seems reasonable to assume larger prey would be eaten if the opportunity existed. Thus, other limits must be imposed; one such limit may be the slow swimming speed of engraulid larvae.

NUTRITIVE VALUE OF PREY OF DIFFERENT SIZES

The nutritive value of larger prey can be illustrated by considering the relation between width of copepods and their weight. Gruzov and Alekseyeva (1970) give a wet weight to length conversion for a group of copepods including species in Calanidae, Paracalanidae, Pseudocalanidae, and other families having a cephalothorax length to width ratio of 2.0-2.8. I transformed their data to show dry weight as a function of cephalothorax width by using the midpoint of their width ratio (2.4) and assuming a water content of 87% (Lovegrove 1966).

This calculation indicated that an increase of 2.5 in width produces an order of magnitude increase in dry weight. Thus, a larva feeding on copepodites 200 μm wide would have to capture 10 times the number of prey to obtain the same ration as one feeding on copepods 500 μm wide (Fig. 6). The effect of a slight increase in width of prey eaten is more marked if the change from feeding on nauplii to copepodites is considered. The change in body width of *Calanus* from nauplius VI to copepodite I is slight even when appendages are included in the measurement (Wiborg 1948a), but the dry weight about doubles. In *Calanus helgolandicus,* the dry weight of nauplius VI is 2.0 μg and that of copepodite I is 4.3 μg (Paffenhöfer 1971). The well-known seasonal and regional variation in copepod weight (Marshall and Orr 1955; Gruzov and Alekseyeva 1970) should be

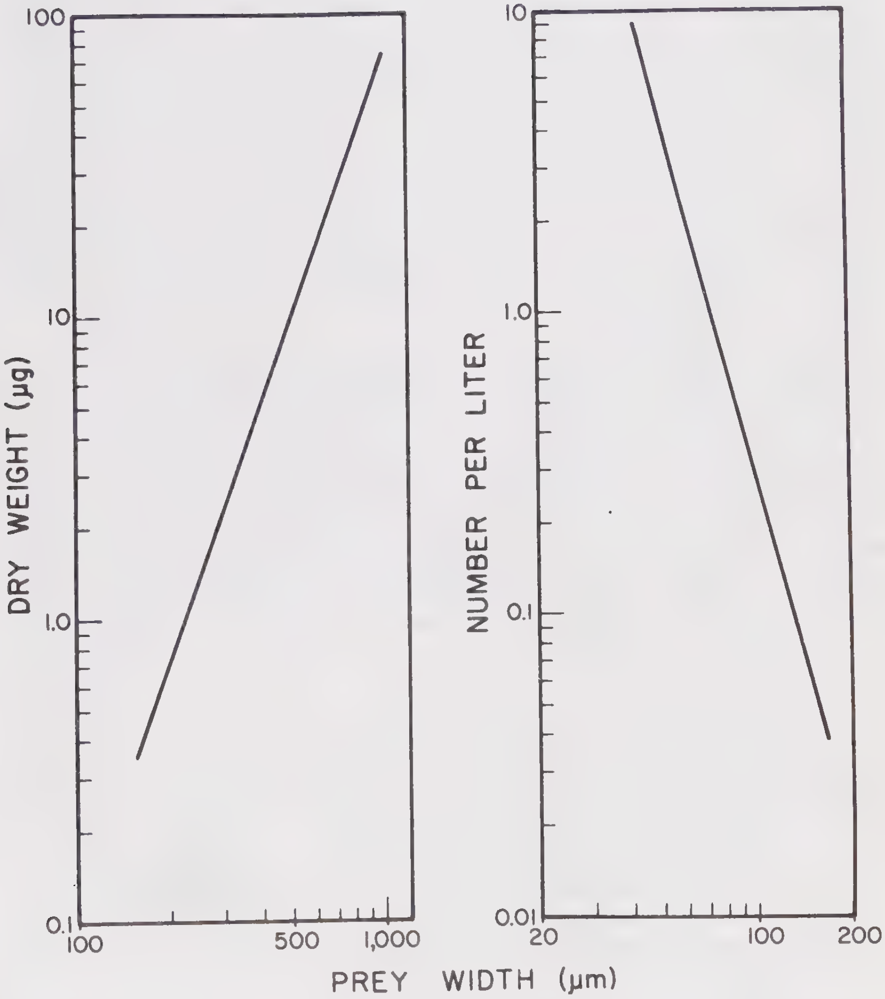

FIG. 6. Left panel, relation between copepod width and dry eight (excluding naupliar stages) calculated from data given by Gruzov and Alekseyeva (1970). Right panel, relation between number of prey per L in the sea and prey width, recalculated from Vlymen (1977).

considered in any study of food size relations in larval fishes.

The necessity for increasing prey size with growth is illustrated by comparing growth rates of larval anchovies (Hunter 1977) and Pacific mackerel (Hunter and Kimbrell, MS) fed different foods (Fig. 7). When anchovies are fed *Gymnodinium* alone, growth becomes asymptotic at about 6 mm whereas when *Gymnodinium* and the rotifer *Brachionus plicatilis* are used, growth becomes asymptotic at about 20 mm and few larvae survive (survival drops from 46% at age 26 days to 6% at age 42 days). Similarly, Pacific mackerel growth slows on a diet of only *Brachionus* and few survive beyond 8 mm at age 15 days. Howell (1973) was able to grow plaice larvae through metamorphosis on *Brachionus* alone, but at a much slower growth rate than when *Artemia* was used, indicating that some species are able to grow through metamorphosis on rather small prey but at a depressed growth rate.

Vlymen (unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA) estimated for larval anchovy the minimum caloric value of prey required to meet energetic needs for parameters in his 1977 paper. The model uses a 12-h feeding day, a temperature of 17°C, and the maximum feeding rate observed in the laboratory (about 10 attacks/min). Gut capacity was not included and consequently the limit was set by the maximum feeding rate. To calculate the minimum caloric value of prey necessary to meet energy needs, Vlymen used the model $E_1 + E_2 + E_3 + E_4 = 0.48\,R$ where:

$E_1 = (5.10 \times 10^{-2})\, L^{3.3237}$ (the basal metabolic rate in calories, where L = length (cm));
$E_2 = 0.19\, L^{4.48}$ (the total energy cost of swimming);
$E_3 = 0.05\, L^{4.48}$ (the total energy cost of feeding attacks at maximum rate during a 12-h day);
$E_4 = 0.29R$ (the energy cost of mechanically processing food, intestinal propulsion, etc).;
$0.48\,R$ (the proportion of the ration (R) available for energetic needs).

The ration at the maximum attack rate was $R = (7.12 \times 10^3)\, C \times S$ where 7.12×10^3 is the total number of attacks at the maximum rate in a day of feeding; C = calories per prey; and S = the success of capture. By substitution he obtained $(3.78 \times 10^{-5})\, L^{3.3237} + (1.77 \times 10^{-4})\, L^{4.48} = C \times S$. The success of capture (S) is a function of age, not length, and is described by the function $S = 93.2 \operatorname{Log}_{10} T - 33.3$ where T is larval age in days. To obtain the minimum caloric value of prey for larvae of various lengths, ages at specific lengths were obtained from laboratory growth rates (Hunter 1976). The origin of the data and the derivation of the parameters used in this model are described by Vlymen (1977).

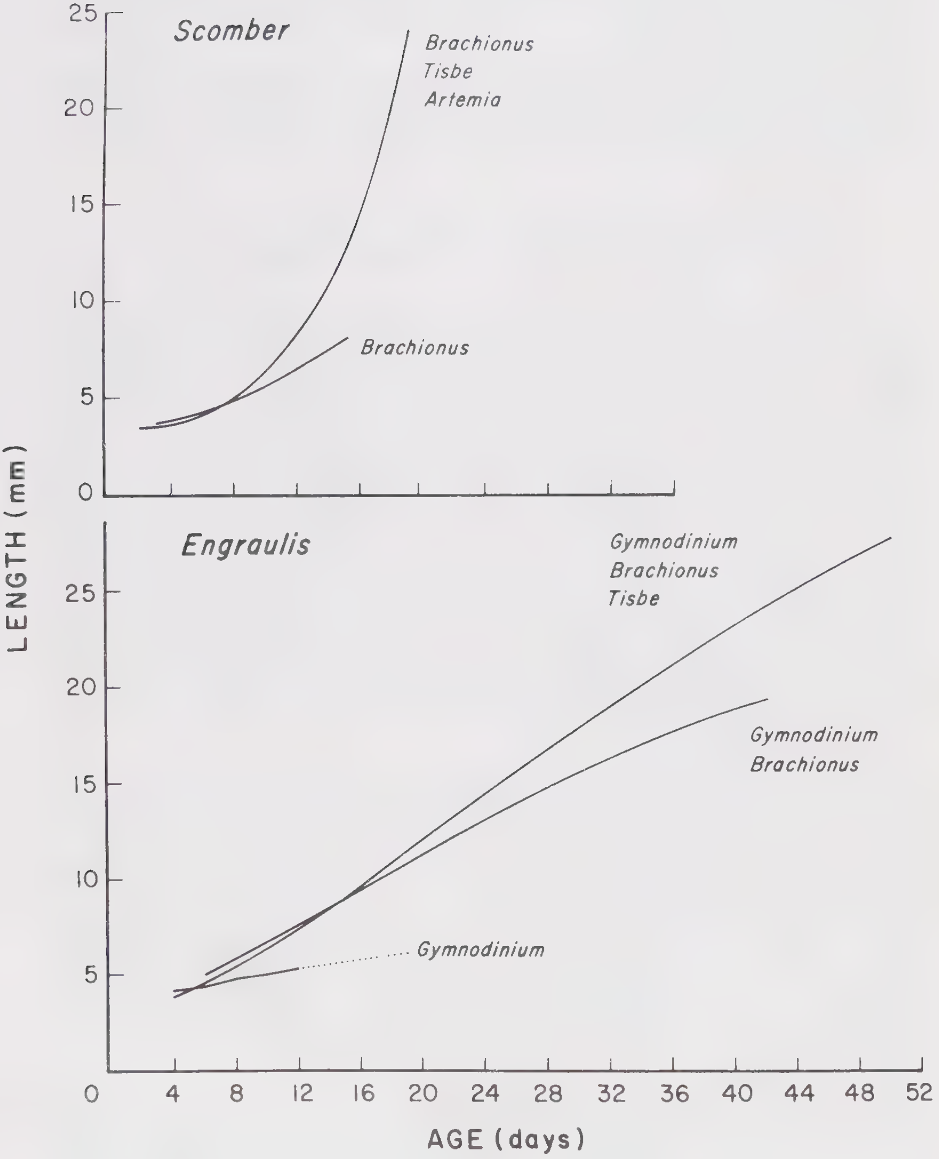

FIG. 7. Laboratory growth rates of *Scomber japonicus* at 22°C fed various foods, from Hunter and Kimbrell (MS), and of *Engraulis mordax* at 16°C, from Hunter (1977). Calorie values of prey were: *Gymnodinium* 0.00005 cal; *Branchionus* 0.0008 cal; and *Artemia* 0.0096 cal (Hunter 1977).

His results are reasonably close to those described above from rearing work. The model predicts no growth beyond a length of 6 mm on prey having a caloric value of *Gymnodinium* and none beyond 14 mm for *Brachionus* (Fig. 8).

Thus, the lower size limit of prey, at least over the first few weeks of feeding, appears to be set by metabolic relations, whereas the upper limit is controlled by mouth size.

Abundance of Food and Food Density Requirements

The density of particles in the sea declines rapidly with increasing size or diameter of the particle (Sheldon, Prakash and Sutcliffe 1972; Sheldon and Parsons 1967). Such a relationship was presented by Vlymen (1977) for particle size distribution from Niskin casts measured with a Coulter Counter by Richard Eppley (Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA) (Fig. 6). Sheldon et al. (1972) pointed out that roughly similar amounts of organic material exist in logarithmically equal size intervals in any water mass; hence, in any sample, many more small particles exist than larger ones. This implies that to feed on larger prey, a larva must search a much greater volume of water and it also may explain why the minimum prey size changes so slowly in larvae that select larger prey.

The density of particles in the size range relevant to larval marine fishes has been studied by a number of workers and their results have been reviewed by Blaxter (1965), May (1974), and Arthur (1977) and are presented here in tabular form (Table 2). These studies indicate that average density in the open sea ranges between 13-40 nauplii per liter and typically between 1-7 copepodites per liter. On the other hand, in enclosed areas such as lagoons, bays, and estuaries, much higher densities are found. Average densities in these areas of naupliar and post-naupliar stages combined can exceed 200 per liter.

Larval fishes have been maintained in the laboratory at various food densities to determine the density of prey required for survival. Some of these density experiments are summarized in Table 3. Most indicate a prey density of 1000-4000 microcopepods/L are required for high survival rates in the laboratory. These results agree in general with what has become standard rearing practice in recent years; in such techniques, the highest densities are used initially and are subsequently reduced to about 1000/L (Houde 1973). Much higher densities are required for very small prey such as phytoplankton. Lasker (1975) found that anchovy larvae required 5000-20,000 *Gymnodinium splendens* cells per liter at 19°C and 20,000 or more at 14°C for significant feeding to occur. Standard rearing

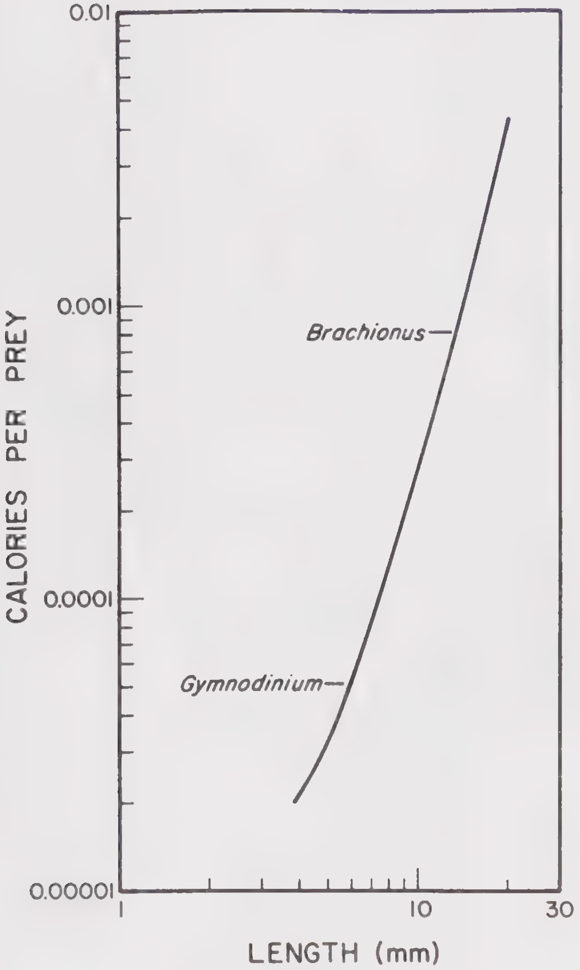

FIG. 8. Relation between minimum caloric value of prey required to meet energy needs of larval northern anchovy at 17°C and larval length. From model developed by Vlymen (1977) and Vlymen (unpublished), see text for explanation. The caloric value of *Gymnodinium* and *Brachionus* is indicated.

TABLE 2. Average[a] densities of microcopepods in the sea.

	Average density of microcopepods (number per liter)				
	Nauplii	Copepod-ites	Total	Location	Author
Open sea	13	2	15	Southeast Coast of Kyushu	Yokota et al. (1961)
	22	36	58[b]	California Current	Beers and Stewart (1967)
	40	5	45[b]	Southern California near shore	Beers and Stewart (1970)
	27	7	34[c]	Eastern Tropical Pacific	Beers and Stewart (1971)
	36	1	37	California Current	Arthur (1977)
Partly enclosed	76	19	95	Azov Sea	Duka (1969)
	—	—	223[d]	Gulf of Taganrog	Mikhman (1969)

[a] Mean for all stations, and years given in publication listed in table.
[b] Includes all copepods passing 202 μm mesh net.
[c] Includes all copepods passing 202 μm mesh net and caught on 35 μm mesh.
[d] Defined as food of *Clupeonella delicatula;* microcopepods account for over 90% of items eaten (Mikhman 1969).

TABLE 3. Food density thresholds for six species of marine fish larvae.

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density No./L	Survival at various food densities: Density No./L	Survival at various food densities: Percent survival	Author
Plaice *Pleuronectes platessa*	5	14	*Artemia* nauplii	50 (larvae)	1,000	72[a]	Wyatt (1972)
					500	72	
					200	54	
					100	32	
Northern anchovy *Engraulis mordax*	10.8	12	Wild zooplankton (nauplii)	10 (eggs)	4,000	51	O'Connell and Raymond (1970)
					900	12	
					90	0.5	
					9	0	
Bay anchovy *Anchoa mitchilli*	76	16	Wild zooplankton (nauplii-copepodites)[c]	0.5-2 (eggs)	1,751[b]	50	Houde (1977 and in press)
					75	10	
					17	1	
Sea bream *Archosargus rhomboidalis*	76			0.5-2 (eggs)	199[b]	50	Houde (1975 and in press)
					28	10	
					11	1	
Lined sole *Archirus lineatus*	38			0.5-2 (eggs)	854[b]	50	Houde (1977 and in press)
					115	10	
					44	1	
Haddock *Melanogrammus aeglefinus*	37.8	42	Wild zooplankton (nauplii)	9[d] (larvae)	3,000	39	Laurence (1974)
					1,000	22	
					500	3	
					100	0	
					10	0	

[a] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).
[b] Estimated food density for indicated survival levels.
[c] Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.
[d] Estimated by adjusting for hatching success.

practice for northern anchovy requires 100,000 or more *Gymnodinium* cells per liter (Hunter 1976b), whereas 1,000 microcopepods per liter appear to be adequate (O'Connell and Raymond 1970).

Density thresholds determined by Houde (1975; 1977; in press) are markedly lower than those of the others listed in the table and are substantially below those used for routine rearing of larval fishes. He attributes his lower thresholds to use of lower stocking densities, general improvement in culture techniques, and frequent daily monitoring and adjustment of food density. He also maintains a dense phytoplankton bloom in his containers which may also contribute in some way to higher survival. Of particular interest is the very low threshold determined for sea bream, emphasizing the importance of specific feeding tactics. This species selects larger prey (Stepien 1976) than the other species studied by Houde, and judging by the density threshold, is much more efficient in finding and catching prey.

In general, the density thresholds determined for larvae in the laboratory are much higher than average microcopepod densities in the open sea, described in the previous section. On the other hand, the high microcopepod densities in enclosed areas are within the range that Houde (1975, 1977) found to support survival and growth. Thus, food may not be as critical for species, such as those he studied, which exist in such areas. Many problems exist in interpreting such laboratory findings and extending them to field conditions. The interactions of stock density, food density, and mortality are problems which may be overcome to some extent by use of low stocking densities and frequent monitoring of food density. Changes in ration with development and prey size distributions in the tank are also critical. The few larvae that survive at very low prey densities may be those that captured, either by good fortune or because of a larger mouth, the few larger prey in the container. Selection of the appropriate criteria also poses problems. Growth as well as survival declines with food availability; this is evident in all the food density studies cited but perhaps best illustrated by Riley (1966), Wyatt (1972) and Houde (1975, 1977). Reduction of growth may be nearly as lethal as starvation because of the increased exposure to predation.

The disparity between most estimates of food densities required by larvae and average densities in the open sea have led to the hypothesis that larvae may be dependent on small-scale patchiness of food. In the sea, large-scale sampling will always tend toward the mean concentration between such patches. Data collected by Yokota et al. (1961) on naupliar abundance provides one of the better examples of patchiness of larval forage because the samples were taken on a scale relevant to larval searching behavior. They counted all the nauplii occurring in 1-liter samples taken at the surface from an area off the southeast coast of Kyushu over 2 yr. The average naupliar density for their 4,730 samples was 13/L. The greatest number in a single sample was 524 and only 2% of the samples accounted for over 20% of the nauplii.

Laboratory experiments on searching behavior discussed previously indicate that larvae have the ability of remaining in patches of food if they find them. The search model of Vlymen (1977) indicated that the average anchovy larva could not exist in the sea if food were distributed randomly. He concluded that first feeding anchovy larvae require a food contagion of $K = 0.17$, where K is the negative binomial, just to meet minimum energy requirements. Thus, to meet minimum requirements, prey would have to be 1.3 times as "crowded" as they would be on the average, if the population had a random distribution (Lloyd 1967).

Lasker (1975) tested the patchiness hypothesis by exposing anchovy larvae to samples of water taken from the surface and from the chlorophyll maximum layers usually 15-30 m below the surface. Feeding by larvae was minimal in samples taken from the surface but extensive feeding occurred in water from the chlorophyll maximum layer when these samples contained prey of about 40 μm at densities of 20,000 to 400,000 prey/L. The prey were primarily the phytoplankter *Gymnodinium splendens;* microcopepods were never at high enough densities to be eaten by the larvae. Houde and Schekter (in press) exposed sea bream to simulated patch conditions in the laboratory by increasing the concentration of microcopepods to 500/L for periods of 2-13 h per day from a background density of 25-50/L. They found that survival at 10 days after hatching of larvae exposed to only 3 h of food at 500/L was similar to that of larvae fed at a constant 500/L. Thus, even very short-term patchiness could enhance survival in this species. Lasker (1975) has considered a much broader time scale; the bloom of *Gymnodinium* had persisted for at least 18 days until a storm obliterated the chlorophyll maximum layer. His measurements after the storm indicated that the density of food was insufficient for feeding.

Ecological Roles

In this section, I define two ecological roles based on the traits discussed in the preceeding sections. These roles, Engrauliform and Scombriform (Table 4), were selected because of their contrasting traits, by firsthand knowledge of the behavior of *Engraulis mordax* and *Scomber japonicus*, and because in the beginning they are of similar size and have similar yolk reserves. To fill in gaps of knowledge, I have used results for other species which I believe fall within these two ecological categories.

TABLE 4. Two contrasting ecological roles for marine fish larvae based on behavioral and physiological traits.

Trait	Relative differences	
	Engrauliform	Scombriform
Spawn		
Contagion of spawn	High	Lower (?)
Food		
Mouth size	Small	Large
Range of food size	Small	Large
Abundance of foods eaten	Higher	Lower
Calories obtained per attack	Lower Higher	Higher
Feeding behavior		
Feeding posture	Sinuous	Rigid
Persistence of attack	Infrequent	Frequent
Feeding capacity	Low	High
Ability to exploit short-term food patch	Low	High
Maneuverability	Low	High
Locomotion and metabolism		
Cruising speed	Slow	Fast
Metabolic rate	Lower	Higher
Social interactions (laboratory)		
Effect of larval density on growth	Low	High
Sibling cannibalism	Rate	Frequent
Time on onset of schooling	Late	Early
Growth	Slow	Fast
Instantaneous mortality	Lower	Higher

Food size preferences may be one of the best diagnostic traits for identifying ecological roles. To feed on large prey requires a large mouth and a greater and more efficient searching effort because of the exponential decline in density with prey size. Greater searching effort may require a faster swimming speed and this in turn implies a higher metabolic rate and energy requirements. Large prey are more efficient in satisfying energy requirements and promote faster growth (Kerr 1971a and 1971b). Faster growth reduces the duration of the larval stage and the time to the onset of schooling. A larva that is more dependent on large prey can ill afford to pass up prey if the first attack fails. Thus, persistence in attack and maneuverability would appear to be essential, and the sinuous mode of feeding seems to lack these characteristics.

The sparid *Archosargus rhomboidalis*, which seems to fit in many respects the scombriform role, is affected much more by laboratory stocking density and is better able to take advantage of short-term patchiness of food than is the engraulid fish *Anchoa mitchilli* (Houde and Schekter 1978). These tendencies are in keeping with the differences in searching power and efficiency of feeding implicit in these roles. Feeding rates and ration also could be expected to vary between these roles but few accurate measurements exist. Owing to the strong effect of food density, larval weight and temperature (Stepien 1976), specific comparisons are not possible. At least in younger larvae satiation mechanisms appear to be lacking. Death from overfeeding in the laboratory has been reported for grunion (May 1971) and the siganid, *Siganus canaliculatus* (May et al. 1974), and I have observed it in larval Pacific mackerel. Northern anchovy maintained at the same food density as mackerel did not die from overfeeding, suggesting a higher feeding capacity in the more active mackerel.

Although the evidence is weak for differences in spawn density that I have associated with these roles, it does make some evolutionary sense. At high spawn densities, suppression of intraspecific effects on growth would be adaptive as well as suppression of sibling cannibalism. Species of slow swimming abilities such as anchovy might require higher initial larval densities to assure the socialization necessary for the onset of schooling, or to form schools of viable size. Finally, Ware (1975) suggests that instantaneous mortality is proportional to growth rate. If Ware's argument is correct, then the slow growth of anchovies relative to mackerel (Fig. 9) is indicative of a lower mortality.

In these comparisons, many assumptions and simplifications were made and the very significant role of temperature was not considered. In a strict sense, such roles should only be defined within specific temperature ranges. Many other possible strategies exist. Those species that hatch from large eggs in a relatively large and mature state, such as flying fish, herring larvae, saury, and many others, do not fit into these categories. The flatfishes show major deviations from either pattern because of the striking changes at metamorphosis resulting in declines in activity and metabolic rate (Blaxter and Staines 1971; Laurence 1975). Another possible role is that of a larva dependent on large prey, but using a relatively passive hunting strategy at reduced metabolic cost and experiencing a slow growth rate. This contrasts with the fast growth, high metabolism, and active hunting of scombroid larvae. This more passive large prey strategy could be relatively common in cold water where metabolic costs are less.

My emphasis has been on specific differences in feeding ecology of larvae because I feel this approach is essential for understanding the cause and effect relationships underlying mortality. The apparent similarities in feeding habits among pelagic larval fishes are striking nonetheless. The characteristics emphasized here, such as preferences for size ranges of copepods, minor differences in larval

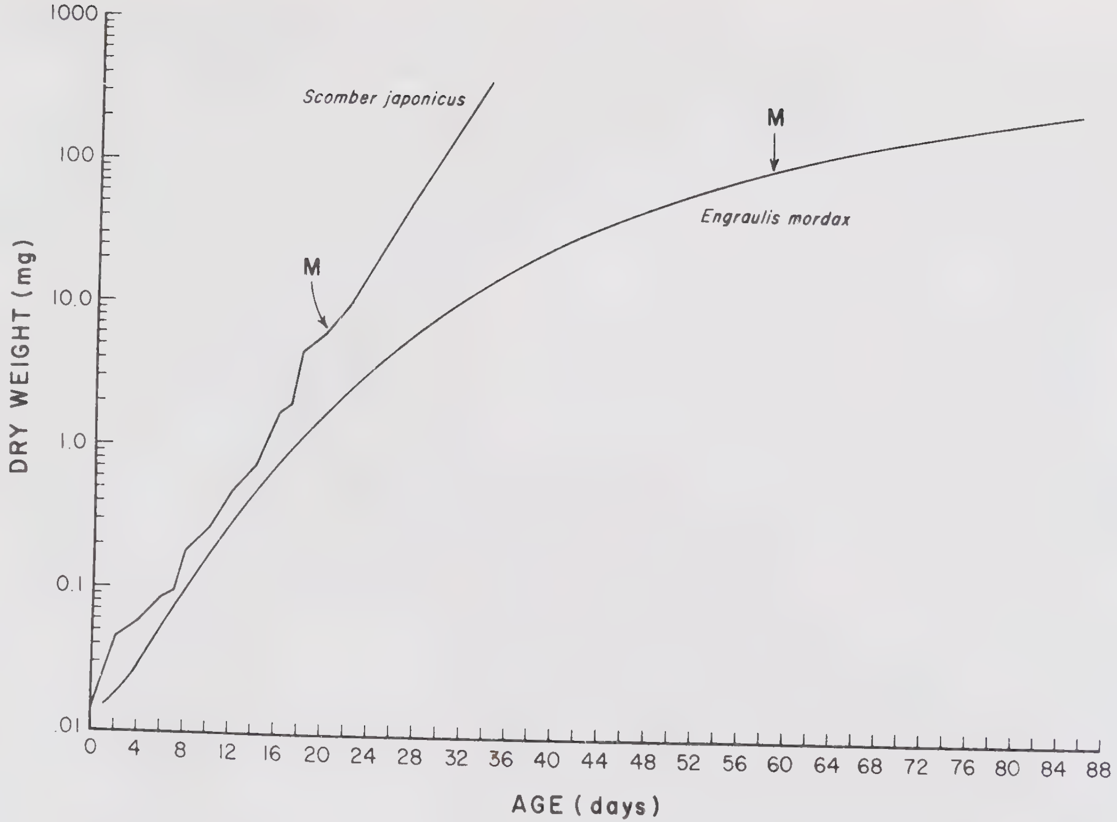

Fig. 9. Growth of larval *Scomber japonicus* and *Engraulis mordax* in the laboratory at 19°C. Data on *Scomber* is a line formed from connecting average length for three experiments and converted to weight by length-weight conversion (Hunter and Kimbrell, MS); data on *Engraulis* is a Laird-Gompertz fit (Hunter 1975) to unpublished rearing data at 19°C; and M indicates age at metamorphosis.

size and yolk reserves, and differences in swimming speed, seem subtle relative to the major differences that exist in feeding ecology of the parents. Nearly all larvae are diurnal, particulate planktivores specializing in the young stages of copepods despite the fact that the feeding habits of the parents include benthic and epipelagic piscivores, filter-feeding and particulate-feeding planktivores, and many other specializations. The feeding habits of larvae, of course, are most similar at first feeding when larvae are least specialized, and distinctions become more obvious as development proceeds and fish approach metamorphosis.

Given proper phase relationships, many species could be dependent on the same food resource. Competition between species is regulated to some extent by the timing of spawning and its relation to the production cycle. In the California Current, peak spawning by the northern anchovy occurs in early spring, whereas peak spawning by the large-mouthed larvae, jack mackerel and Pacific mackerel, occurs later, although spawning of all three species broadly overlaps (Kramer and Smith 1970a, 1971). Vertical partitioning of the water column has not been discussed but is a tactic of major importance. *Scomber* larvae seem to be more closely associated with the upper surface layers than clupeoid larvae, whereas hake are located at greater depths (Ahlstrom 1959; Nellen and Hempel 1970). It is possible that the rapid metabolism, fast growth, large prey tactics of scombroids may be designed for near-surface existence and possibly the slow growth, large prey tactics of hake are limited to cooler or deeper waters. Clearly, vertical distributions of larvae and their foods need detailed attention.

Sources of Mortality, Approaches

A critical period for survival occurring around the time of first feeding has long been hypothesized as a possible determinant of year class strength (Hjort 1914; May 1974; Vladimirov 1975). Hjort's critical period concept, as restated by May (1974), is that the strength of year classes in marine fishes is determined by availability of planktonic foods shortly after the yolk supply has been exhausted. Low feeding success, low resistance to starvation, small size, and immaturity of larvae at this time suggest that they would be more vulnerable to starvation death than at any other time, but the evidence from estimates of natural mortality is inconclusive (May 1974). Although physiological and behavioral criteria indicate the highest vulnerability at yolk absorption, it is also the time when larvae feed upon the smallest and therefore most abundant food supply. Events in later life such as the necessity to feed on larger but less abundant prey, disruption of food patches by storms, and failure to form viable schools could also be sources of mortality. In the anchovy, a major risk may be involved in the shift from very small prey such as nauplii and phytoplankton to larger copepodites. This risk would be faced by larger-mouthed larvae at a much earlier age. This risk can be hedged to some extent if larvae continue to feed on smaller prey and take larger copepods when available, which seems to be a basic strategy as evidenced by the slow increase in minimum prey size in all species. Sooner or later, these large prey must be eaten or growth will be slowed, as laboratory work has demonstrated, and retarded growth leads to greater exposure to predation (Murphy 1961).

To isolate causes of natural mortality of larval fishes, estimates must be made of incidence of starvation and predation over the spawning range and these losses compared to estimated rates of mortality. Such models must account for egg mortalities of up to 29% per day and larval mortality rates of 2-10% per day (Jones and Hall 1974). Predation is probably the most common cause of mortality during the egg and yolk-sac stage, although other causes have been suggested (Vladimirov 1975). Predation by fishes on eggs is detectable by stomach examination because the chorion is relatively resistant to digestion but may be difficult with larvae such as small 3- to 5-mm anchovy where digestion is so rapid that larvae are unidentifiable in less than 2 h (Hunter, unpublished data). The study of predation by arthropods and other predators that injure or grind prey will also be difficult. Owing to the diversity of potential invertebrate predators, bioassays of samples from predator communities might be a productive approach, perhaps using large plastic enclosures containing fish larvae. It seems unlikely much progress could ever be made using a species-by-species analysis.

Studies of starvation in the sea seem to offer a better opportunity for isolating a cause of mortality than those of predation because of the difficulty of direct observation and detection of predation. Laboratory work indicates that incidence of starvation can be identified by chemical, morphological and histological criteria (Balbontin, de Silva and Ehrlich 1973; Ehrlich 1974; O'Connell 1976; Ehrlich, Blaxter, and Pemberton 1976). If absolute criteria are to be used, histological techniques may be preferable because deterioration of cell and tissue structure appears to be less affected by laboratory rearing and is independent of size (O'Connell 1976).

Morphometric techniques are desirable because they can be applied routinely over the spawning range of a species and can be easily incorporated into standard ichthyoplankton analysis. They have been used by Shelbourne (1957) and Blaxter (1971) to assess condition of sea-caught larvae, but Blaxter's work indicates that their application should be confined to a relative assessment. He found in herring that body depth and condition factor changed with starvation in the laboratory, but larvae captured in the sea had a lower condition factor than those dying of starvation in the laboratory. I obtained nearly identical results with northern anchovies using body depth (Hunter, unpublished data). Thus, the most practical approach for assessment of starvation on a population basis may be morphometric analysis calibrated in terms of starvation using histological analysis of sea-caught specimens. Finally, intensive studies in the laboratory and at sea are essential for defining ecological roles and causes of mortality, but in the long term these studies must lead to identification of parameters that can be measured routinely over the spawning range of the species.

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Discussion

FISHELSON

What do you think science may contribute after 5 yr or more to stock maintenance from the point of view of larvae?

HUNTER

I think we'll know the probable effect of the environment on year-class strength or at least know whether or not it is even practical to approach the problem from the standpoint of larval mortality. We have many field studies going on. We'll be able to assess the proportion of starving larvae in the sea in the next few years and perhaps separate starvation from predation as a cause of mortality.

BARDACH

When you talk about recruitment, do you talk about recruitment to the fishery?

HUNTER

Yes.

BARDACH

When is the onset of fishing?

HUNTER

When the fish are about 1 yr old and about 10 cm in length.

MURPHY

I don't think they're fully recruited until they're 2 yr old.

BARDACH

How does this compare with the Peruvian stocks?

MURPHY

Full recruitment occurs at 1 yr, but heavy fishing mortality starts at about 6 mo.

FUJIYA

You said something about cannibalism. Is that real cannibalism or just biting?

HUNTER

It's real cannibalism. Mackerel larvae eat fish about half their size.

BLAXTER

There must be a size hierarchy before that occurs.

HUNTER

It depends on the species: barracuda, for example, become cannibalistic at about 4 mm long when the larvae are all nearly the same size, and they prefer fish by the time they're 10 mm.

MURPHY

What is the thinking now with respect to the size of the larvae when the relative survival for a year-class is more or less stabilized? From what you told me, it's not just when they're starting to feed.

HUNTER

Correct. Paul Smith of our laboratory has preliminary estimates of mortality now of fish up to 20 mm for 25 yr. You can see a higher mortality at the onset of feeding and a great deal of differential mortality in different years, but the year-class strength is not established even at 20 mm.

MURPHY

You're talking about numbers of fish, and those have a tremendous variance. The estimate for a given year is pretty wide.

BLAXTER

How does growth in your tanks compare with that in the sea?

HUNTER

We're beginning to get data on growth of anchovies in the sea by counting daily rings on the otoliths. Differences between laboratory and sea growth can be as great as the difference caused by a 2-3°C difference in rearing temperatures. In general, larvae in the sea grow slower than larvae reared in the laboratory at the same temperature, but occasionally we find some samples in which sea-caught larvae appeared to be growing faster than laboratory-reared larvae.

BLAXTER

You might think there'd be stronger selection for size in the sea than in a tank where there are no predators.

HUNTER

Yes. Growth may appear to be faster in the sea because of predation.

LILEY

When you do have more information about the larval ecology and feeding behavior, how do you see its being applied? Are you not looking at the possibility of culturing these pelagic fish?

HUNTER

No.

LILEY

What do you think could be the long-term application of this? This helps you to make predictions, but I'm wondering if there are things that you can go into and do.

HUNTER

Our objectives are to learn what is causing the large fluctuations in the annual number of recruits in fish populations. We feel that if we had a better idea of the mechanisms, we could better manage fish stocks. Nobody as far as I know has yet been able to solve these problems.

HASLER

Is the Peruvian anchovy coming back?

MURPHY

They started to recover and then apparently faltered and are falling off. The data from Peru aren't as available as they used to be, but I understand they closed anchovy fishing and turned everybody on to sardines and mackerel.

HASLER

That fishery makes such a huge contribution to the world's protein supplies that it would seem important to focus on that.

HUNTER

Yes. The world's largest fisheries are based on these clupeoids, which is why we're working on them.

MYRBERG

How does your knowledge of these species provide information relative to those species that are cultured? Can we learn something from this that can be applied to those species that are well known in culture?

HUNTER

Many of us have reared fish larvae for a number of years, and I think collectively the techniqes from our own and others' research are beginning to follow certain patterns. A reservoir of information exists, and many of the techniques that are almost intuitive now were developed by hard work in many laboratories over the last 10 yr. For example, the rule of one nauplius per mL didn't always exist.

MAY

It seems to me that fish species that are now commercially cultured are primarily the species that are easy to rear through the larval stages. The kinds of fishes that John is talking about are not commercially cultured anywhere, but I think the information he and other people are gathering will provide the basic knowledge which will enable these species to be cultured in the future. I don't know if it will ever happen on a commercial scale, but it may, and if it does, it will depend fairly heavily on the kind of basic knowledge that's being accumulated now.

HUNTER

There are many incidental findings that may be useful for rearing other species. For example, we found the best way to reduce cannibalism was to rear mackerel at the highest temperature possible. Cannibalism stops at metamorphosis when they start schooling, and you can double the survival by reducing the time to metamorphosis.

FISHELSON

Is it possible then that we can use heated waters of reactors and power plants to farm in the sea, using large ponds in which we can grow the small larvae till they pass the cannibalistic stage and then let them out?

HUNTER

People working on tropical fishes have greater problems with water chemistry than those working on temperate, coldwater species. When I speak of warm water I mean about 22-23°C, which is warm for Pacific mackerel but is not warm by tropical standards.

BLAXTER

Surely cannibalism is partly an artifact of the crowding in the tank, isn't it?

HUNTER

Yes, although cannibalism is common even in adult scombroids. I don't think there's much doubt that if a scombroid encounters another it would eat it if it were the correct size. But I think spawn is much less dense than that of clupeoids and encounters may be infrequent.

MAGNUSON

I think that about 10% of the stomach contents of adult skipjack captured on the high seas consist of their own juveniles. You gave two strategies for pelagic larvae. Are these essentially the only two strategies? Or is there some continuum?

HUNTER

I think many larvae may fall into these classes, but hake would be a good example of one that does not, and there are many others. A continuum may exist, but other variables, especially temperature, would have to be considered before all differences could be accounted for in a continuous pattern. Some larvae that feed on large prey grow slowly and may have a more passive feeding strategy than scombroids, but these seem to be adapted to cooler temperatures. A continuum seems likely because the range of feeding strategies is more limited in larvae than adults. Nearly all larvae are diurnal, particulate planktivores specializing in the young stages of copepods.

BLAXTER

In the past the work on rearing larvae, at least Shelbourne's work, has led to a technology for rearing flatfish for farming; turbot are now at the point of being farmed commercially. The technology all comes from the general work that was done in the sixties, and so there's been a fairly rapid practical spinoff from that work. Of course it's for valuable fish; it's a luxury market.

MURPHY

If we succeed in artificially spawning milkfish, there's some guidance about how to go about rearing the larvae.

BLAXTER

I think with *Brachionus* as a food almost any species could be reared.

HUNTER

I think the critical element is a 240-μm-diameter particle. In other words, a food is needed as a substitute for *Artemia* nauplii, because many larvae do not grow well when fed *Artemia* nauplii, although plaice and others do. I think many major improvements can be made in the *Brachionus* system, and I think it's a waste of time to worry about artificial foods of the size of *Brachionus*.

ATEMA

I recall the famous story on the East Coast where they used to raise lobsters in hatcheries up to the fourth stage and then release them. Nobody has ever shown that the operation was successful. I suspect they released them in the wrong place, but another possibility is that if they raised them to the sixth stage, would they have been successful? I wonder about that in your fish stituation. How large is the dangerous window?

BLAXTER

All the early work on releasing plaice and cod never improved the fishery. In fact the only case where there apparently was some improvement was when Dannevig released cod into the Skagarak.

8035

SEXUAL MATURITY, BATCH FECUNDITY, SPAWNING FREQUENCY, AND TEMPORAL PATTERN OF SPAWNING FOR THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, DURING THE 1979 SPAWNING SEASON

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ABSTRACT

Fifty percent of anchovy females reach sexual maturity by 96 mm standard length (95% confidence level 94-97 mm). Spawning batch fecundity, estimated from counts of hydrated eggs, was an exponential function of female weight. ($\ln Y = 4.2886 + 1.6281 \ln X$, where Y = number of hydrated eggs and X = female weight less ovary weight in grams). In the Los Angeles Bight the proportion of the population spawning/day (incidence of day-old post-ovulatory follicles) declined from 13.4% of the females in January-February to 10.0% in March-April and fell to 3.4% by June. Incidence of atresia in ovaries increased as the frequency of spawning declined. The percentage of females classed as post-spawning on the basis of the atretic condition of the ovary was 0.3% in January-February and 12% in March-April. Spawning of anchovy in Monterey Bay had nearly ended in March, and 71.9% of the females were classed as post-spawning.

The incidence of females with new post-ovulatory follicles and with hydrated eggs indicated that by sunset eggs were completely hydrated and spawning began; spawning reached a maximum between 2200-2300 hours and ended by 0200 hours. At 0600 hours females destined to spawn the next night began to hydrate eggs.

RESUMEN

El 50% de las anchovetas hembras alcanzan la madurez sexual al llegar a los 96 mm de longitud normal (nivel de confianza de 95%, 94-97 mm). La fecundidad del grupo desovante, calculado mediante recuento de óvulos hidratados, fue una función exponencial del peso de la hembra ($\ln Y = 4.2886 + 1.16281 \ln X$, donde Y = el número de óvulos hidratados y X = el peso de la hembra menos el peso del ovario en gramos). En la Bahía de Los Angeles la proporción de la población desovante diaria (incidencia de folículos post-ovulatorios de un día) disminuyó del 13.4% de las hembras durante enero-febrero al 10.0% en marzo-abril, y bajó al 3.4% en junio. La ocurrencia de atresia en los ovarios aumentó mientras que la frecuencia del desove disminuía. El porcentaje de hembras clasificadas como post-desovantes, a base de la condición atrética del ovario, fue 0.3% en enero-febrero y 12% en marzo-abril. El desove de anchoveta en la Bahía de Monterey casi había terminado en marzo, y 71.9% de las hembras fueron clasificadas como post-desovantes.

La presencia de hembras con nuevos folículos post-ovulatorios y con óvulos hidratados indicaba que, a la hora de la puesta del sol, los óvulos estaban completamente hidratados y se iniciaba el desove. El desove alcanzó un máximo entre las 2200-2300 horas y terminó a las 0200 horas. A las 0600 horas las hembras destinadas a desovar la siguiente noche empezaron a hidratar óvulos.

INTRODUCTION

To assess anchovy spawning biomass using the gonad-egg model of Parker (1980), spawning frequency and batch frequency must be estimated. This paper provides data on spawning frequencies and fecundity for the 1979 spawning season of the northern anchovy, *Engraulis mordax*. We also estimate the probability of sexual maturity of females as a function of length, examine the atretic state of the ovary using histological criteria, and reexamine the relation between the reproductive state of females and time of day. We combine our data with those of Hunter and Goldberg (1980) to establish general relationships between batch fecundity and weight and between time of day and spawning.

METHODS

Female anchovy were collected during two major survey periods in the Los Angeles Bight: January 26-February 16, 1979 (61 collections, total females = 619) and March 22-April 14, 1979 (48 collections, total females = 601). An additional set of three collections was taken June 9-19 in the Los Angeles Bight (33 females), and a set of five collections (150 females) was taken in Monterey Bay during March 20-22, 1979. Most of the fish were taken at night using a midwater trawl, but in January-February, 15 collections were from lampara nets set by commercial fishing vessels, and all the Monterey samples were from commercial vessels.

Our plan was to measure and sex a minimum of 25 fish per sample, weigh and preserve the first 10 mature females for histological examination, and all immature specimens until the quota of 10 mature females was obtained. In practice, the number of fish sexed remained constant, but the number of mature females preserved varied. In some cases, we increased the sample size of females to compensate for fewer samples, and in others a high incidence of immature females and a highly biased sex ratio reduced the number of mature females to less

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than 10. In April 1979, we sampled a single area throughout one night to determine the consistency of spawning frequency within a single aggregation of schools. In this case we set the quota at 20 mature females/sample to increase the precision of the estimate. The variation in sample size of females has produced some statistical problems that have not been resolved. For this reason, error terms are not provided for spawning frequency estimates.

Batch fecundity was estimated for 32 females taken in January-February and 12 females taken in March-April by counting the number of hydrated eggs in a weighed sample of the gonad (Hunter and Goldberg 1980). The females used showed no evidence of recent spawning (no post-ovulatory follicles).

Many of the smaller females taken in January-February 1979 had small ovaries. Small females that had spawned within 24 hours could be confused with immature females if a judgement were made on the basis of ovary size alone. To avoid a histological examination of every immature ovary, we examined a subset of 160 females ≤ 12 g (body weight less ovary weight) to establish a weight criterion for immaturity. For these females we calculated the ratio of ovary weight/(body weight less ovary weight), grouped the data into eight ratio classes ($N = 20$ females per class), and calculated the percent of females in each class that were mature on the basis of histological criteria. Probit analysis (Finney 1952) was used to fit a line to the regression of maturity probability on $\log_{10}$ of the ratio of body weight/ovary weight (Figure 1). This analysis indicated that for females of 12 g or less, the probability of maturity was less than 5% when the gonad weight/body weight ratio ≤0.01. Henceforth, all females ≤12 g were considered immature if the ratio was 0.01 or less; all other females were examined histologically.

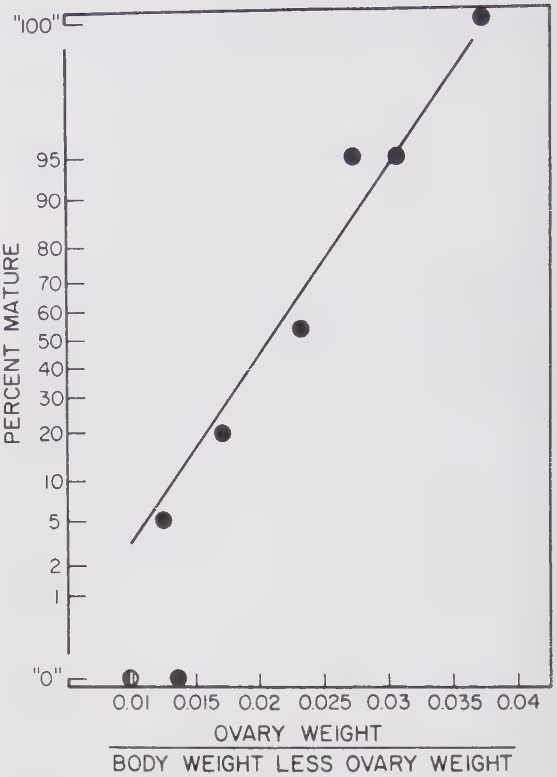

Figure 1. Percent of mature females (body weight ≤ 12 g) in eight classes of the ratio, ovary weight/(body weight less ovary weight);($N = 2$ females/class): percentage plotted at the mean ratio within each class. Females taken in January-February 1979 in the Los Angeles Bight. Line fit using probit analysis; equation for line is $Y = 21.52 + 9.837\ X$, where Y = % maturity in probits (Finney 1952) and $X = \log_{10}$ of the ratio.

HISTOLOGICAL CLASSIFICATION

Spawning Frequency

For estimation of spawning frequency, females were examined histologically and classified into the five classes defined by Hunter and Goldberg (1980).

Hydrated. Ovaries with many hydrated eggs (eggs enlarged by fluid uptake just prior to ovulation) and no post-ovulatory follicles. Spawning considered to be imminent.

Age 0 day. New post-ovulatory follicles, showing no sign of degeneration. Hydrated eggs may occasionally be present. Elapsed time from spawning less than 24 hours.

Age 1 day. Regressing post-ovulatory follicles showing degeneration as described by Hunter and Goldberg (1980). Elapsed time from spawning equal to or greater than 24 hours but less than 48 hours.

Non-spawning (mature). Ovaries with many yolked oocytes; may contain post-ovulatory follicles in advanced stages of degeneration which cannot be readily distinguished from other atretic structures. May include females with highly atretic ovaries. Elapsed time from spawning 48 or more hours.

Immature. Few or no yolked oocytes. No atresia present in ovary other than late-stage corpora atretica. (A weight criterion was used to classify immaturity in some females ≤ 12 g; see methods section.)

We also determined the atretic condition of the ovaries of all mature female anchovy taken in 1979 including those with post-ovulatory follicles and hydrated eggs. This analysis provided an additional measure of the spawning potential of the population because rates of ovarian atresia would be expected to increase in ovaries as the end of spawning approaches and all yolked oocytes are resorbed. During the initial phase of the atretic process, the oocyte is resorbed and yolk globules are broken down and resorbed by hypertrophying granulosa cells of the follicle (the α stage of Bretschneider and Duyvené de Wit 1941; Lambert 1970). In the next stage (ß stage), all the yolk is gone, there remains a rather compact structure with one or more cavities (corpora atretica); the tissue is composed of granulosa and theca cells with penetrating blood vessels. The degeneration of the granulosa and theca cells begins in this stage. In the third and fourth stages (stages γ and δ of Lambert 1970), regression of theca and granulosa cells continues thereby reducing the size of the follicle, and a yellow-brown pigment appears. This pigmented condition is characteristic of late-stage corpora atretica.

The incidence and extent of the above atretic oocyte stages in the ovary and the presence of yolked eggs were used as criteria for five classes of atretic ovarian condition (Table 1). All ovaries were assigned to one of the classes on the basis of the criteria given in the table. The presence of late corpora atretica was not used as a criterion because they may persist in the ovary for a long time and occur in ovaries regardless of the incidence of other atretic stages. The earliest atretic stage (α) was the most useful character because the size of the oocyte is still apparent.

We also include in the table the percentage of all mature females taken in 1979 that had post-ovulatory follicles (ages 0-1 day) combined with those with hydrated eggs. This percentage, defined as total spawning activity, decreased with an increase in atretic condition, indicating, as expected, that atretic condition of the ovary and spawning activity are correlated.

SEXUAL MATURITY

All females collected in February 1978 were mature (Hunter and Goldberg 1980); whereas only 64% of the females taken in January-February 1979 were mature, and 91% were mature in March-April 1979. Data for 1979 were grouped by 5-mm standard length (SL) classes, percent maturity calculated for each class (Table 2), and the probability of maturity regressed on the $\log_{10}$ of the mean length of females in each class using probit analysis (Finney 1952). The estimated length at 50% maturity was the same for January-February, 96 mm (95% CI 94-97 mm) as for March-April, 96 mm (95% CI 94-98 mm). A good fit was obtained between probability of maturity and length in both sets (Figure 2).

The maturity lines for the two surveys in 1979 had different slopes because females 105-119 mm had a higher probability of maturity in March-April than they did in

TABLE 2

Percent Maturity of Female Northern Anchovy in the Los Angeles Bight by Length Class for February 1978, January-February 1979, and March-April 1979.

Length class (mm)	February 1978		January-February 1979		March-April 1979	
	N	% mature	*N*	% mature	*N*	% mature
71- 75	2	100	4	0		
76- 80	5	100	19	5		
81- 85	1	100	56	11		
86- 90	4	100	69	29	2	50
91- 95	3	100	80	48	7	86
96-100	6	100	70	56	46	67
101-105	8	100	58	76	120	80
106-110	17	100	39	82	134	94
111-115	47	100	46	87	117	96
116-120	53	100	33	94	59	100
121-125	36	100	31	94	48	100
126-130	24	100	50	100	40	100
131-135	35	100	44	100	19	100
136-140	25	100	13	100	15	100
141-145	18	100	5	100	3	100
146-150	9	100	1	100		
151-155	2	100	1	100		100
156-160					1	
Σ	295		619		611	

TABLE 1

Characters Used to Classify the Atretic Condition of Ovaries of Northern Anchovy[1] and the Total Spawning Activity within Atretic Ovary Classes.

		Incidence of *α* stage[4] atresia in:					
				Yoked oocytes[3]			
Atretic ovary class	Total spawning activity[2]	Yolked oocytes present	Unyolked oocytes	Small	Large	Incidence of ß stage atresia[4]	Other diagnostic characters
No atresia	0.36	+	0	0	0	0	
Minor atresia	0.21	+	*	*	0	+	
Early post-spawning	0.10	+	*	+	+	*	Less than 50% all yolked oocytes are in α stage atresia
Post-spawning	0	+	*	+	+	*	Greater than 50% all yolked oocytes are in α stage atresia.
Late post-spawning	0	0	*	0	0	+	

[1] + = present; 0 = absent; and * = may occur.

[2] Proportion of all mature females within each class having hydrated eggs or post-ovulatory follicles (ages 0 and 1). Combined data for January-February 1979 and March-April 1979 in Los Angeles Bight and March 1979 in Monterey Bay. Number of females in each of the five classes were: 592 (no atresia), 323, 92, 46, and 49 (late post-spawning).

[3] Distinction between atretic large and small yolked oocytes can be made only early in α stage of atresia when size differences are apparent, but yolked oocytes can be separated from unyolked throughout the α stage because of staining differences in hematoxylin and eosin preparations.

[4] α and ß stages of atresia are defined in text.

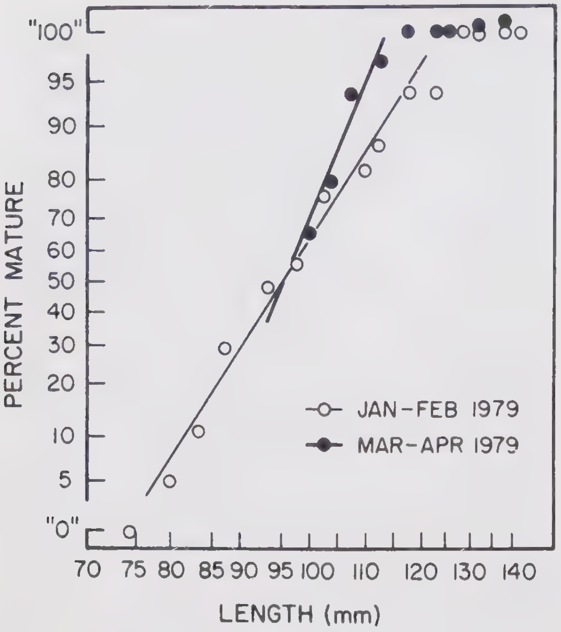

Figure 2. Percent maturity of female anchovy taken in Los Angeles Bight in January-February 1979 (open circles) and March-April 1979 (solid circles) as a function of standard length. Points are percent of females that were mature in each 5-mm class of length and are plotted at mean length within class. Equations for lines are: January-February, $Y = -29.793 + 17.572\ X$ and March-April, $Y = -48.30 + 26.899X$; where Y = % maturity in probits (Finney 1952) and $X = \log_{10}$ standard length.

January-February 1979, whereas the probability of maturity for smaller females remained the same. The change in slope of the maturity line during 1979 and the difference in maturity between 1978 and 1979 could be caused by differences in sampling or statistical uncertainties. It could also be a measure of a real difference in the maturity-length relation as the spawning season progressed.

FECUNDITY

The spawning batch fecundity of female anchovy, on a unit weight basis, varied from 389 hydrated eggs/g female weight less ovary weight to 444 eggs/g, and the mean for all fecundity estimates was 421 ± 36 eggs/g (Table 3). MacGregor (1968) and Hunter and Goldberg (1980) concluded that for assessment work, the mean number of eggs per unit weight (relative fecundity) was sufficient and presented their data in that form. The existence of a larger data set (Table 4), based on hydrated eggs, permitted a reexamination of the fecundity weight relation. We regressed the number of hydrated eggs per female on female weight less ovary weight, using the combined data for 1978 and 1979. The geometric mean regression (Ricker 1973) yielded the equation $\ln Y = 4.183 + 1.620 \ln X$, where Y = number hydrated eggs, X = female weight less ovary weight, $r^2 = 0.51$ and $s^2_{y \cdot x} = 0.1295$ (the 99% confidence intervals for the slope did not include 1; Figure 3, upper). The form of this relation was similar to the one between gonad weight and female weight for mature nonspawning females with eggs of 0.65 mm (major axis) in the most advanced mode (Hunter and Goldberg 1980). To compare the two equations, we estimated ovary weight using their equation, $\ln G = -4.213 + 1.069 \ln W + .555\ D \ln W$ (G = ovary weight, W = female weight, and D = major egg axis [.65 mm]) and multiplied the estimated ovary weight by the mean number of advanced eggs per gram of ovary (8,630 ± 921); Hunter and Goldberg 1980). The two equations give similar results although based on different females and methods of calculation (Figure 3, lower). The regression equation appears to be a reliable method of estimating batch fecundity for females of the central subpopulation of northern anchovy and is more accurate than expressing fecundity on a unit weight basis. The error in using relative fecundity becomes substantial for females larger than 25 g (Figure 3, lower).

TABLE 3

Relative Batch Fecundity (Eggs per Unit Weight) for Females with Hydrated Eggs Taken in Each Survey and Calculated from Regression Equation for Batch Fecundity where X = Mean Weight of All Females Taken in Survey.

				Relative batch fecundity		
	Weight of all mature females (less ovary)		Mean for females with hydrated eggs		From regression equation, where X = mean weight of all females[3]	
Survey period	N	$X \pm 2SE$[2] g	N	$X \pm 2SE$[2] eggs/g (without ovary)	weight less ovary eggs/g	weight with ovary eggs/g
February 1978[1]	328	17.29±0.74	23	389±59	409	389
January-February 1979	394	16.40±0.67	32	444±57	396	376
March-April 1979	558	15.50±0.39	12	423±67	383	364
All data	952	15.87±0.30	67	421±36	388	369

[1] From Hunter and Goldberg (1980).

[2] ±2 times standard error of mean.

[3] $\ln Y = 4.183 + 1.620 \ln X$, where X = female weight less ovary and $\ln Y = 4.100 + 1.620 \ln X$, where X = female weight with ovary. Estimate of total egg ($\ln Y$) increased by factor ½ $s^2_{y \cdot x} = 0.0647$ to correct for bias in taking antilog (Beauchamp and Olson 1973).

TABLE 4

Batch Fecundity of Northern Anchovy from Counts of Hydrated Eggs: Data for Three Surveys in the Los Angeles Bight.

Female weight less ovary (g)	Ovary weight (g)	Total hydrated eggs	Survey[1]
9.3	1.171	3822	1
9.3	1.406	2874	2
9.8	1.202	3538	1
10.8	1.190	2894	2
10.8	2.109	6178	2
11.7	1.485	3604	2
11.9	1.202	5950	1
11.9	1.704	4201	2
12.5	1.038	4625	2
12.7	1.697	4001	3
12.9	2.155	6386	1
13.1	1.995	4742	2
13.1	1.586	4585	3
13.4	1.888	4556	3
13.7	1.575	6288	1
14.2	3.083	8818	3
14.6	1.287	3270	1
14.7	1.352	3822	3
14.9	1.523	4455	3
15.2	2.473	5852	3
15.3	2.114	5279	2
15.4	0.835	3234	1
16.0	2.210	4336	1
16.0	1.235	4592	1
16.0	2.586	7040	3
16.1	2.058	4862	2
16.4	2.750	8922	3
16.6	2.622	5677	2
16.6	5.624	13363	2
17.2	3.275	7895	2
17.2	2.148	7258	1
17.3	2.473	5744	2
17.3	3.883	7958	3
17.9	2.369	8216	1
18.1	3.092	8978	3
18.5	2.819	6420	2
20.1	3.296	9447	1
20.2	5.298	9595	2
20.3	2.798	7714	2
20.4	3.017	6181	1
20.6	3.996	13266	1
21.3	4.539	9159	2
21.4	2.910	6292	2
21.9	4.253	12461	1
22.8	5.479	11902	2
22.9	3.988	9366	1
22.9	1.990	2794	2
23.0	4.047	12742	2
23.4	4.159	8354	2
23.5	4.812	16662	1
23.7	6.366	14196	2
23.7	6.031	15310	2
24.3	4.131	12515	2
24.4	1.906	5392	1
24.5	3.556	10217	2
24.7	3.793	10621	2
24.8	5.561	14037	3
25.5	5.686	11577	1
25.7	5.648	13955	2
26.3	4.228	8548	2
26.8	8.049	20797	2
26.9	2.956	5972	1
28.0	9.645	23044	2
28.1	6.388	14668	2
30.4	1.967	6292	1
31.2	4.793	10577	1
31.9	3.796	9251	1

[1] 1 = February 1978, $N = 23$;
2 = January-February 1979, $N = 32$;
3 = March-April 1979, $N = 12$.

We used counts of hydrated eggs to estimate spawning batch fecundity because it was a more rapid and more accurate method than counting the number of eggs in the most advanced mode (Hunter and Goldberg 1980). This method requires that fecundity be calculated in terms of female body weight, less gonad weight, because hydration of the ovary significantly alters the total weight of the female. On the other hand, to assess spawning biomass, fecundity must be expressed in terms of total weight. Our fecundity measurements can be converted to a total weight basis using the ratio of the two body weights for females without hydrated eggs (w/W, Table 5). This ratio was 0.95, and it varied little between seasons, regions, or years. The fecundity equation was re-estimated from the data in Table 4 using total female weight (female weight less ovary weight/0.95) as the independent variable. The geometric mean regression (Ricker 1973) of numbers of hydrated eggs (Y) on total female weight (female weight less ovary/0.95; X) was $\ln Y = 4.100 + 1.620 \ln X$, where $r^2 = 0.51$, and $s^2_{y \cdot x} = 0.1295$.

We believe it is preferable to use the regression equation to estimate batch fecundity for assessment of spawning biomass rather than the average relative fecundity. In Table 3, we use the equation to estimate the relative batch fecundity for the mean of the weight of all mature females taken in each survey, and we compare these values to means calculated on a unit weight basis. Regression estimates of relative fecundity using the mean weight of females taken in a survey differ by 5-11% from the average relative fecundity for the same survey because of differences in the weights of hydrated females within the samples used for the unit weight averages.

FREQUENCY OF SPAWNING

Spawning frequency is best estimated from the incidence of day-old post-ovulatory follicles (day 1), because incidence of females with hydrated eggs or new post-ovulatory follicles are affected by the time of capture and sexual composition of the school (Hunter and Goldberg 1980). The ovaries of 13.4% of the mature females taken in January-February 1979 (Table 6) and 10.0% of those taken in March-April 1979 (Table 7) had day-old post-ovulatory follicles. Thus, on the average, female anchovy in the Los Angeles Bight spawned every 7-10 days during the three peak months of spawning in 1979. Only 3.5% of the 29 females taken in June 1979 in the Los Angeles Bight has post-ovulatory follicles. Although the sample size is small, these data indicate that the frequency of spawning had declined by June.

Incidence of day-old post-ovulatory follicles reported by Hunter and Goldberg (1980) were 15% for February 1978 and 14.2% for a small sample taken in March 1977. Thus, data for the peak spawning months in 1979 was in keeping with past results. As in the past study, no relation existed between incidence of day-old post-ovulatory follicles and size of the mature females, time of day, or locality within the Los Angeles Bight.

Ovaries of females taken in Monterey Bay in March 1979 were distinctly different: none contained day-old post-ovulatory follicles, and only two (1.3%) had new post-ovulatory follicles (day 0; Table 8). Thus, spawning had nearly ended in Monterey Bay by March, whereas it continued at a high level to the south in the Los Angeles Bight. Abundance of anchovy larvæ and eggs taken in the 1979 CalCOFI survey also indicated that spawning ended in Monterey by March but continued in the Los Angeles Bight and south along the Mexican coast (Stauffer and Parker 1980).

In a recent study Laroche and Richardson (in press) point out that the northern subpopulation of the northern anchovy off Oregon and Washington probably spawn fewer times than the central subpopulation we studied. They noted degeneration of oocytes in ovaries of females

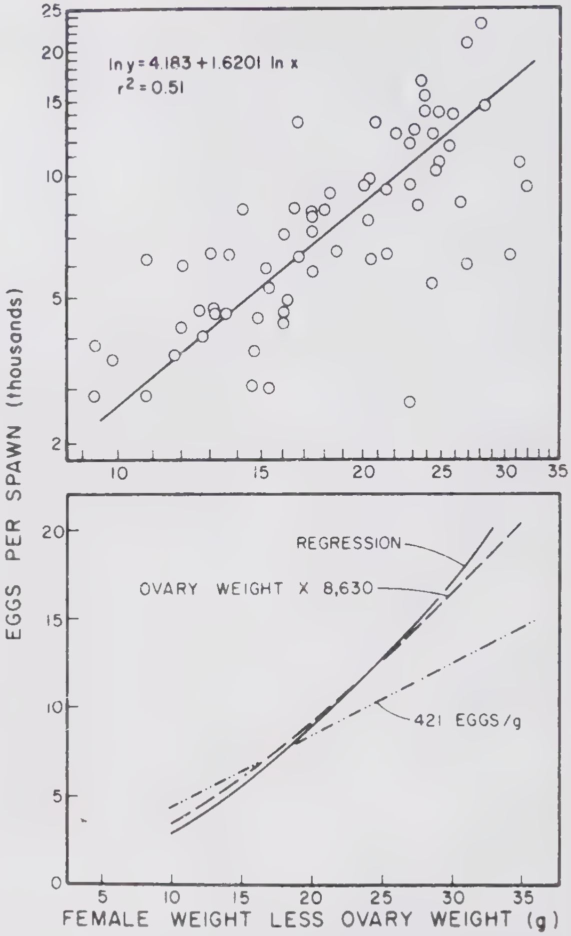

Figure 3. Batch fecundity of northern anchovy taken in the Los Angeles Bight, 1978-79. Upper panel: regression of ln total number hydrated eggs on ln female weight (less ovary weight). Lower panel: three methods of estimating batch fecundity are compared; solid line from regression in upper panel; dashed line, ovary weight (G) times mean number eggs (non-hydrated) in advanced mode (8630 ± 921) where $1nG = -4.213 + 1.069\ 1nW + D\ (0.555\ 1nW)$. W = female weight (less ovary) and D = size of eggs (0.65 mm; from Hunter and Goldberg 1980), and dash-dot line is mean relative fecundity for 1978-79, 421 eggs/g female weight (less ovary)

TABLE 5

Mean Body Weight of Females[1] with (W) and without (w) the Ovary Included and Regression of W on w for Various Survey Periods and Regions.

Survey and region	Total body weight (W) in g			Body weight less ovary (w) in g			$W = -a + bw$ where:		
	N	X	s	X	s	w/W	a	b	r^2
February 1978 (Los Angeles Bight)	69[2]	20.2	8.05	19.2	7.45	0.950	.514	1.078	0.997
January-February 1979 (Los Angeles Bight)	355	17.1	7.15	16.2	6.64	0.947	.409	1.077	0.998
March-April 1979 (Los Angeles Bight)	536	16.2	5.10	15.5	4.70	0.957	.520	1.081	0.995
March 1979 (Monterey)	145	19.3	6.64	18.5	6.18	0.959	.516	1.073	0.997
All data combined	1099	17.2	6.36	16.4	5.90	0.954	.450	1.076	0.997

[1] Only sexually mature females included: females with hydrated eggs excluded.

[2] Gonad weight not available for all females examined.

TABLE 6

Reproductive State of Female Northern Anchovy Collected in the Los Angeles Bight in January-February 1979.

			Number of females in various reproductive states				Total females	
				Post-ovulatory follicles		Mature no evidence of spawning		
Collection number[1]	Month and day	Time of day (hours)	Hydrated eggs	0 day[2]	1 day		Mature	Immature
3040	2 10	18.03	–	2	1	5	8	3
3034	2 09	18.08	4	–	4	2	10	0
3025	2 07	18.12	3	–	3	4	10	0
3006	1 27	18.23	–	1	1	3	5	6
3017	2 03	18.27	1	–	1	8	10	0
3019	2 04	18.27	7	–	–	3	10	0
3000	1 26	18.37	–	–	–	1	1	12
3020	2 06	18.73	1	–	1	8	10	0
3012	1 29	18.88	–	–	–	2	2	5
3007	1 27	19.12	–	–	1	3	4	7
3046	2 13	19.17	–	–	1	7	8	1
3041	2 10	19.32	2	–	–	7	9	10
3018	2 03	19.48	5	–	1	4	10	0
3026	2 07	19.70	–	–	–	10	10	0
3001	1 26	20.05	–	–	–	2	2	8
3013	1 29	20.18	1	2	–	–	3	2
3035	2 09	20.27	2	1	–	6	9	0
3021	2 06	20.38	2	2	3	2	9	0
3042	2 10	20.63	3	–	–	6	9	3
3029	2 08	20.67	2	1	5	2	10	0
3008	1 27	20.93	–	–	1	2	3	12
3002	1 26	21.30	–	–	–	–	0	10
3036	2 09	21.62	2	–	2	6	10	0
3014	1 29	21.67	–	–	2	3	5	1
3022	2 06	21.82	–	5	1	4	10	0
3043	2 10	21.85	–	1	–	9	10	0
3030	2 08	22.27	1	1	–	8	10	0
3003	1 26	22.33	–	–	–	–	0	11
3009	1 27	22.45	–	–	–	1	1	16
3027	2 07	22.72	–	–	3	7	10	0
3037	2 09	23.02	–	–	–	3	3	0
3044	2 10	23.30	–	–	–	5	5	1
3015	1 29	23.55	–	3	–	7	10	0
3023	2 06	23.70	–	3	–	–	3	0
3010	1 27	23.75	–	–	–	6	6	7
3031	2 09	00.05	–	–	2	8	10	0
3028	2 08	00.12	–	1	3	6	10	0
3038	2 10	00.52	–	1	1	8	10	0
3004	1 27	00.72	–	–	–	–	0	14
3011	1 28	00.78	–	–	–	7	7	8
3045	2 11	00.95	–	2	–	–	2	0
3024	2 07	01.12	–	3	–	2	5	0
3032	2 09	01.63	–	1	4	5	10	0
3039	2 10	02.03	–	1	3	6	10	0
3016	1 30	02.90	–	1	–	1	2	2
3033	2 09	03.00	–	4	1	5	10	0
2006	2 05	03.42	–	1	1	8	10	0
2001	1 27	03.50	–	2	–	1	3	7
2005	2 02	04.00	–	–	–	7	7	3
2002	1 27	04.17	–	–	1	4	5	8
2004	1 30	04.50	1	–	1	3	5	5
2007	2 07	04.50	–	–	–	5	5	5
2010	2 16	04.50	–	–	–	9	9	1
2003	1 27	05.00	–	–	–	2	2	11
2008	2 07	05.00	1	1	4	4	10	0
1002	2 08	05.00	–	–	–	2	2	9
2009	2 16	05.33	1	1	1	7	10	0
1004	2 12	05.50	–	1	–	7	8	2
1001	2 07	05.50	–	2	–	1	3	14
1003	2 08	06.00	–	–	–	3	3	11
1005	2 15	06.00	–	–	–	1	1	10
S			39	44	53	258	394	225
%			9.9	11.2	13.4	65.5	63.6	36.4

[1] Collection numbers in 1000 and 2000 series were commercial lampara sets; 3000 and 4000 were midwater trawl.

[2] Females with hydrated eggs and day 0 post-ovulatory follicles included in this class.

TABLE 7

Reproductive State of Female Northern Anchovy Collected in the Los Angeles Bight in March-April 1979.

			Number of females in various reproductive states				Total females	
				Post-ovulatory follicles		Mature no evidence of spawning		
Collection number[1]	Month and day	Time of day (hours)	Hydrated eggs	0 day[2]	1 day		Mature	Immature
3064[3]	4 07	18.80	2	1	4	13	20	0
3054	4 03	18.92	1	–	1	8	10	0
3079	4 12	18.92	2	1	–	7	10	11
3082	4 13	18.92	–	–	4	6	10	–
4008	3 24	19.15	–	1	2	11	14	1
4001	3 22	19.25	–	–	–	11	11	0
3050	4 02	19.33	–	1	3	6	10	0
4004	3 23	19.57	3	1	1	9	14	1
3071	4 08	20.25	1	–	–	9	10	0
3055	4 03	20.35	–	–	3	7	10	0
3083	4 13	20.35	2	–	–	8	10	1
3058	4 05	20.43	–	–	2	8	10	0
3073	4 09	20.50	–	–	–	10	10	0
3065[3]	4 07	20.57	1	2	1	16	20	0
3047	4 01	20.60	–	–	3	7	10	0
3060	4 06	20.72	2	–	1	7	10	0
4009	3 24	21.30	5	8	–	1	14	1
3074	4 09	21.75	–	–	1	9	10	0
3072	4 08	21.78	–	1	–	9	10	0
3059	4 05	22.00	–	2	2	6	10	0
4005	3 23	22.05	5	3	2	5	15	0
3048	4 01	22.12	–	–	2	4	6	0
3066[3]	4 07	22.30	1	7	2	9	19	0
3061	4 06	22.50	1	2	1	6	10	0
4002	3 22	22.67	–	2	2	11	15	0
3057	4 04	22.83	–	1	–	7	8	2
3077	4 11	22.87	–	–	–	11	11	1
4010	3 24	23.42	–	2	2	10	14	1
3075	4 09	23.50	–	1	–	9	10	0
3067[3]	4 08	00.02	–	7	1	12	20	0
3062	4 07	00.03	–	1	1	8	10	0
4006	3 24	00.38	–	2	1	7	10	0
3051	4 03	00.48	–	–	3	7	10	0
3076	4 10	00.90	–	2	–	8	10	0
3080	4 13	01.10	–	–	1	4	5	18
3049	4 02	01.13	–	–	2	8	10	0
3078	4 12	01.57	–	–	–	10	10	0
3063	4 07	01.58	–	1	1	9	11	0
3068[3]	4 08	01.67	–	5	1	14	20	0
3084	4 14	02.98	–	4	–	5	9	1
4007	3 24	03.08	–	–	1	12	13	2
3069[3]	4 08	03.33	–	5	1	13	19	0
3081	4 13	03.42	–	–	1	9	10	0
3052	4 03	03.62	–	3	–	7	10	0
4003	3 23	03.65	–	1	1	9	11	2
3070[3]	4 08	04.92	–	4	2	13	18	1
2026	3 23	05.00	–	–	–	–	–	10
3053	4 03	05.05	–	–	–	10	10	0
Σ			26	71	56	405	558	53
%			4.7	12.7	10.0	72.6	91.3	8.7

[1] Collection numbers in 1000 and 2000 series were commercial lampara sets, 3000 and 4000 were midwater trawl.

[2] Female with hydrated eggs and day 0 post-ovulatory follicles included in this class.

[3] Collection is part of a 7-collection series taken in same locality on same night.

TABLE 8

Reproductive State of Female Northern Anchovy Collected in Monterey Bay, California, in March 1979.

			Number females in various reproductive states				
				Post-ovulatory follicles			
Collection number	Month and day	Time of day (hours)	Hydrated eggs	0 day	1 day	Mature no evidence of spawning	Total mature females[1]
2014	3 21	02.30	–	1	–	29	30
2020	3 22	03.15	–	–	–	30	30
2017	3 21	03.45	–	–	–	30	30
2023	3 22	04.15	–	1	–	29	30
2011	3 20	05.00	–	–	–	30	30
Σ			0	2	0	148	150
%				1.3		98.7	100

[1] All females judged sexually mature, but many ovaries in post-spawning condition (see Table 9).

taken in the peak month of July and spawning in the northern subpopulation occurs only from mid-June to mid-August. We examined a small sample of 25 females taken in four research trawl catches taken off Oregon July 18-21, 1977. Ovaries of ten of these females (40%) had new post-ovulatory follicles and four (16%) had day-old post-ovulatory follicles. Twenty-three of the ovaries from these females (92%) exhibited no or only minor atresia, but the ovary from one female was in the early post-spawning condition and that from another in the late post-spawning condition. The latter female had clearly completed spawning for the season. On the basis of this evidence we suggest that the spawning frequency during peak periods of spawning is about the same for the northern as for the central sotck (about once a week), but the northern stock may be limited to about four spawnings per year because of the short duration of the spawning season.

INCIDENCE OF ATRESIA

In January-February 1979, when the frequency of spawning was the highest (13.4%), only 0.3% of the mature females were classed as post-spawning on the basis of ovarian atresia, whereas in March-April 1979, when spawning frequency had declined to 10.0%, 14% of the mature females were classed in one of the three post-spawning stages and 5% clearly were incapable of further spawning (Table 9). In Monterey during March, little spawning occurred, and 71.9% of the females were classed in one of the three post-spawning stages. Thus the incidence of ovarian atresia was inversely correlated with the frequency of spawning, and this indicates that the decrease in the frequency of spawning during the season may be caused by a cessation of spawning. In other words, the interval between spawning may be a biological rhythm having a period of about a week, and the change in the observed spawning frequency may be caused by cessation of spawning by some females in the population rather than changes in the interval between spawning in individual females.

TABLE 9

Incidence of Atretic Classes of Ovaries in Mature Female Northern Anchovy Taken in the Los Angeles Bight and Monterey Bay in 1979.

		Percentage of Females[2]				
Region and month	N^1	No atresia	Minor atresia	Early post-spawning	Post-spawning	Late post spawning
Los Angeles Bight January-February	394	64.4	35.3	0.3	0	0
Los Angeles Bight March-April	558	57.7	28.3	9.0	1.4	3.6
Monterey Bay March	149	10.8	17.3	27.3	25.3	19.3

[1] All mature females.
[2] Stages of atresia defined in methods.

TEMPORAL PATTERN OF SPAWNING

The seven trawl samples taken during a single night in the same locality (March-April 1979, Table 6) provide an illustration of the temporal pattern of spawning within a single group of schools. The percent of females with hydrated eggs decreased from 10% at sunset to zero by midnight, whereas the number of females with new post-ovulatory follicles increased sharply at 2100 hours and varied between 25 and 35% throughout the rest of the night (Figure 4, upper). The incidence of new post-ovulatory follicles in this series was consistently higher than the mean of all collections taken in March-April 1979 (13%, Table 6). Thus, on this particular night, more spawning may have occurred in this group of schools than was typical for all schools in the Los Angeles Bight in March-April. The frequency of day-old post-ovulatory follicles ranged from 5 to 20% but did not vary with time of day; the mean was 9%, close to the average (10%) for the March-April survey period as a whole.

The temporal pattern of spawning for all surveys combined (February 1978, January-February 1979, and March-April 1979) was similar to the one for a single night. Percent of females with hydrated eggs declined

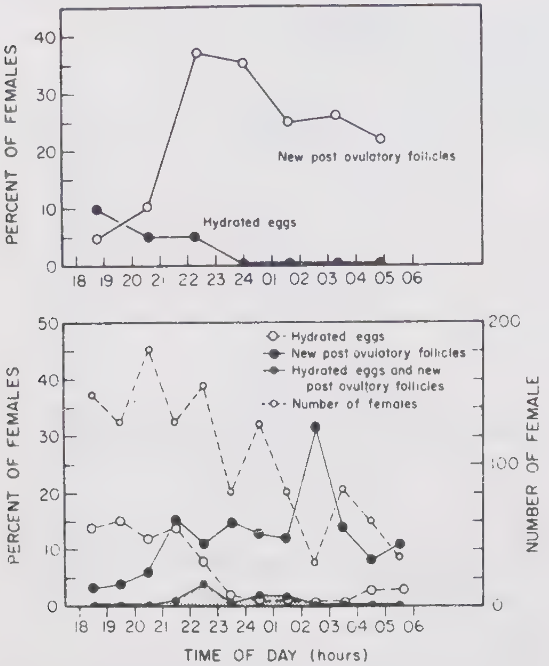

Figure 4. Percent of females in various reproductive stages as a function of time of day. Upper panel: percent of females with only hydrated eggs and females with new post-ovulatory follicles. Samples of 18-20 females taken over a single night at the same locality in the Los Angeles Bight in April 1979. Lower panel: percent of females with only hydrated eggs, only new post-ovulatory follicles, and with both hydrated eggs and new post-ovulatory follicles (shaded area), as a function of time of day. Data are from surveys in the Los Angeles Bight (1978-79). Number of females in each hour class (upper dashed lines) ranged from 35-183.

from about 14% at sunset to 0 at 0100 hours. The occurrence of females with new post-ovulatory follicles increased sharply at 2100 hours and varied between 10-15% throughout the rest of the night (Figure 4, lower). These combined data reveal two additional patterns not resolved in smaller sample sizes: a reappearance of females with hydrated eggs around 0500-0600 hours and the occurrence of females with both hydrated eggs and new post-ovulatory follicles. The reappearance of females with hydrated eggs indicates that hydration for the next night of spawning began in the early morning. The process probably continued throughout the day, resulting in females being ready to spawn at sunset. This view is supported by the fact that our histological examination of hydrated ovaries collected between 0500-0600 hours indicated that they were in the early stages of hydration (characterized by the disappearance of the nuclear membrane, diffused nuclear elements lying in one pole of the eggs, and only partial fusion of yolk globules into the large plate-like bodies).

The best indicator of the time of spawning may be the occurrence of females with both hydrated eggs and new post-ovulatory follicles, because these females were caught while spawning. Their low frequency in the collections indicates that spawning was completed rapidly, and the time of occurrence indicates that the period of maximum spawning occurred between 2100 and 0200 hours, with a peak between 2200 and 2300 hours (Figure 4, lower, shaded area).

On the basis of these results, nightly pattern of spawning in anchovy can be divided into three periods: early spawning period (1800 to 2100 hours), some spawning occurs but the ovaries of most reproductively active females are in the hydrated state; maximum spawning (2100-0200 hours), most females spawn (females with hydrated eggs decline to 0 and females with new post-ovulatory follicles reach the maximum number for the night); and post-spawning (0200-0600 hours), little or no spawning occurs and females destined to spawn the next night begin hydration.

DISCUSSION

This study provided the first quantitative estimate of the size threshold for sexual maturity in female northern anchovy. Clark and Phillips (1952) reported that only a few females mature at 90-100 mm SL, about 30% mature at 100-200 mm, and 50% at 130 mm, whereas Brewer (1978) and Hunter and Goldberg (1980) found significant numbers of mature females less than 90 mm. The present study provided functions from which the probability of maturity can be estimated for any length. The slope of maturity line changed somewhat over the spawning season, but the length at 50% probability of maturity remained the same.

Data collected on the occurrence of female anchovy with hydrated eggs and post-ovulatory follicles in the Los Angeles Bight were similar to those presented by Hunter and Goldberg (1980) for February 1978. The mean interval between spawnings was about 7 days in their study, and it ranged from 7-10 days during the peak spawning months in the present study. The larger number of observations in the present study, combined with past data of Hunter and Goldberg (1980) allowed us to calculate a weight function for batch fecundity and enabled us to describe in greater detail the temporal pattern of spawning behavior.

This paper has provided the reproductive data needed for biomass assessment using the model of Parker (1980). It also indicates needed refinements for future surveys and alternate sampling procedures. That the spawning frequency in Monterey Bay was distinctly different from that of the Los Angeles Bight emphasizes the importance of obtaining samples representative of the entire central subpopulation. Error terms need to be developed for spawning frequency estimates when sample sizes are highly variable. In addition to the incidence of day-old post-ovulatory follicles, the incidence of females with new post-ovulatory follicles or hydrated eggs could be used as a measure of spawning frequency, if appropriate weights were developed for the time of sampling. If anchovy could be sampled during the day, it might be possible to use females with hydrated eggs alone as the measure of spawning frequency. This is an attractive alternative to use of post-ovulatory follicles because it would cost less, as histological examination would not be required.

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Kenneth Mais (California Department of Fish and Game) provided most of the samples of female anchovy. Carol Kimbrell (Southwest Fisheries Center) provided analytical and editorial assistance and Robert Salomons (SWFC) collected anchovy, estimated fecundity, and provided other assistance.

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SPAWNING INCIDENCE AND BATCH FECUNDITY IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*[1]

J. Roe Hunter[2] and Stephen R. Goldberg[3]

ABSTRACT

Histological criteria were developed to age postovulatory follicles from examination of laboratory-spawned northern anchovy and used to estimate the frequency of spawning of natural populations. One-day-old, postovulatory follicles were the preferred estimator of spawning frequency; 48 hours after spawning postovulatory follicles could not be consistently identified because of their rapid degeneration; and the occurrence of postovulatory follicles less than 24 hours old was affected by hour of sampling and sexual composition of the school. The nightly spawning incidence was estimated to be 16±4% of the northern anchovy population in February and 12% in March. Thus, females spawned about every 6-8 days during the peak of the breeding season. The rate of oocyte development corresponded with this reproductive rate, indicating that a new mode of yolked oocytes matured about once a week. Nearly all eggs in the most advanced mode in the ovary were spawned in one night and the number of eggs spawned was estimated to be 389±59 eggs/g of female (ovary-free wet weight). The high spawning frequency and the prolonged breeding season of the northern anchovy indicate that total fecundity may be limited by food availability and energy reserves.

Ichthyoplankton surveys have become one of the standard methods for estimating biomass of marine fish populations. At high latitudes many fishes produce a single spawning batch per year (Qasim 1956) and spawning biomass may be directly estimated from total fecundity and production of eggs and larvae. Multiple (fractional) spawning fishes are characteristic of subtropical and tropical seas (Nikolsky 1963) and estimation of spawning biomass from egg and larval production is dependent upon the number of spawnings per year and the number of eggs per spawning. At present, no adequate method exists for estimating these two parameters for pelagic, multiple spawning fishes.

Past methods have employed measurements of size-frequency distribution of yolked oocytes (usually eggs >0.2 mm in diameter). Eggs are often distributed in one to three modes and the number of eggs in the most advanced mode has been assumed to be equal to the number of eggs produced per spawning (Clark 1934; MacGregor 1968). Another approach has been to count all yolked oocytes in reproductively active females and to assume that these are equal to the number of eggs spawned in a season (Macer 1974). Neither approach provides conclusive evidence for the number of spawnings nor total egg production. All eggs in the most advanced mode may not ovulate (Clark 1934; Yamamoto and Yamazaki 1961) and atresia may reduce the number of eggs per spawning (Macer 1974; Ivankov 1976). Further, the total number of yolked oocytes may not provide an estimate of total fecundity because some of the small unyolked oocytes, not included in such counts, could mature later during the same breeding season.

It has long been known in teleost fishes (Cunningham 1898) that at ovulation a remnant of the ovulated follicle (empty or postovulatory follicle) remains in the ovary. Postovulatory follicles are believed to be transitory because of their rarity in field-collected material (Wheeler 1924; Yamamoto 1956; Gokhale 1957; DeVlaming 1972; Goldberg 1977; Andrews[4]), but actual measurements of their longevity are rare because the time of spawning must be known. Yamamoto and Yoshioka (1964), using *Oryzias latipes* which spawns every 3 days, reported postovulatory follicles were barely distinguishable on the third day after spawning. They suggested that the frequency of spawning

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[1] Supported in part by the Marine Research Committee of the State of California.

[2] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[3] Department of Biology, Whittier College, Whittier, CA 90608.

[4] Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. manuscr., 88 p. Stanford University, Stanford, CA 94305.

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FISHERY BULLETIN: VOL. 77, NO. 3, 1980.

could be determined by the presence of postovulatory follicles but the estimate would have to be made soon after spawning. Through techniques of Leong (1971) it was possible to induce spawning in the northern anchovy, *Engraulis mordax*, in the laboratory, making it possible to characterize the histological degeneration of postovulatory follicles on a time basis. Thus, it seemed feasible that spawning frequency of natural populations of *E. mordax* could be estimated from incidence of postovulatory follicles in females once the period in which they could be detected was established. Moreover, once recently spawned fish were identified, the rate of maturation of subsequent egg batches as well as the number of eggs produced per batch could be estimated.

The objectives of this study were to establish the detection period for postovulatory follicles in northern anchovy and to estimate the incidence of natural spawning through histological examination of these structures. In addition, by using this information to guide our selection of specimens, we provide a new estimate of the number of eggs released per spawning or batch fecundity, and the time required for subsequent spawnings. Previous estimates for anchovy based on frequency distributions of yolked oocytes include those of MacGregor (1968) and Norberg.[5]

METHODS

The period over which postovulatory follicles can be detected in the ovary was determined from anchovy held in the laboratory. Groups of anchovy reared to sexual maturity were induced to spawn using the method of Leong (1971). A total of 119 females were sampled; fish were killed at the time of spawning and thereafter at 24-h intervals up to 9 days after spawning. Ovaries were fixed in Bouin's fixative or 10% neutral buffered Formalin[6] and embedded in Paraplast. Histological sections were cut at 6 μm and stained with Harris' hematoxylin followed by eosin counterstain, Masson's trichrome, periodic acid-Schiff reagent, or Heidenhain's iron hematoxylin. A classification system for postovulatory follicles was established and laboratory specimens were classified without prior knowledge of their age to estimate the accuracy of the technique. Field samples were then classified using the same criteria. Three field collections of anchovy females from the Southern California Bight were examined to determine the frequency of spawning in natural populations: 3 commercial purse seine samples of 38-65 females each from March 1977; 4 research trawl samples of 1-11 females from September 1977; and 29 research trawl samples of 10 or 11 females from February 1978 (Figure 1).

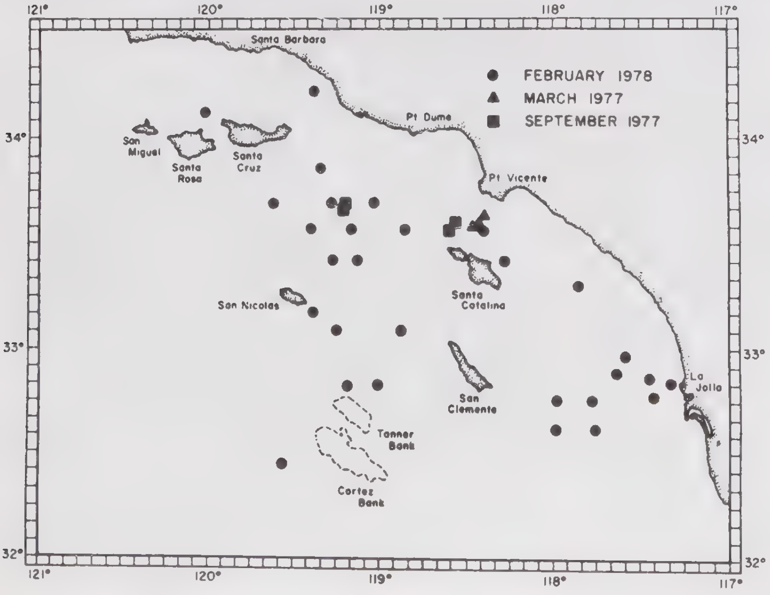

FIGURE 1.—Location of samples of female northern anchovy taken off southern California in March and September 1977 and February 1978.

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[5] Norberg, R. H. 1975. Investigations on the fecundity of northern anchovy, jack mackerel and Pacific mackerel. Unpubl. manuscr., 23 p. Calif. Dep. Fish Game, 350 Golden Shore, Long Beach, CA 90802.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The number of eggs per mode was estimated for 117 of the field-caught specimens by fixing a weighed sample in Gilson's fluid and determining the size-frequency distribution of yolked oocytes (MacGregor 1968; Macer 1974). One-hundred and fifty of the oocytes >0.20 mm on the major axis were measured to the nearest 0.05 mm from each sample and all the remaining oocytes (>0.20 mm) were counted. We shall use "diameter" to refer to these measurements but since anchovy eggs are longer than wide, it is not a diameter in a strict sense but the major axis of an oblate spheroid.

The form of the distribution of egg diameters within an ovary was similar to those illustrated for other multiple spawning fishes (Macer 1974). Distributions varied from ones composed of two to three distinct modal groups of eggs to ones with only a single mode. Even in those with very distinct modal groups the tails of adjacent modes often overlapped. We used the program NORMSEP (Abramson 1971) to separate modal groups, estimate the mean egg diameter within a mode, and estimate iteratively the number of eggs within a mode. Although one must arbitrarily assume egg diameters within a mode are normally distributed, the program does eliminate some of the subjectivity in judging the range of diameters to include within a mode and how the tails of adjacent modes should be proportioned.

Just prior to ovulation and spawning the modal group of eggs about to be spawned takes up fluid and swells to three or four times its former volume (Fulton 1898). These hydrated eggs greatly increase the ovary weight and increase the total weight of the female. To avoid this bias in female weight we used female weight less ovary weight (ovary-free wet weight) to express fecundity-weight relations. We also provide fecundity estimates based on total weight in tabular form so that conversions can be made if desired.

CLASSIFICATION OF OVARIES

Ovaries of laboratory matured females that had spawned within 24 h in all cases contained postovulatory follicles. They were similar in appearance to those described for a variety of teleosts (Cunningham 1898; Wheeler 1924; Bowers and Holliday 1961; Yamamoto and Yoshioka 1964; Moser 1967; Scott 1974). In specimens killed 0-6 h after spawning, postovulatory follicles consisted of irregularly shaped structures composed of columnar follicle cells and an underlying connective tissue theca (Figure 2A, B). In some cases the columnar cells had hypertrophied slightly. The lumen characteristically contained eosinophilic granules of uncertain origin.

Degeneration was pronounced in material examined 24 h after spawning. The postovulatory follicle (Figure 2C) had greatly shrunken or collapsed on itself, vacuoles had become common, and walls of the follicle cells were no longer distinguishable (Figure 2D). The granular material that was observed in postovulatory follicles taken at the time of spawning was still present but not as abundant. The prominent underlying connective tissue theca seen in new postovulatory follicles was no longer distinct. Degeneration had progressed further, 48 h after spawning. The follicle was one-half to one-fourth smaller than at 24 h, the lumen was very small or indistinguishable, eosinophilic granules were absent, and nuclear sizes were greatly reduced.

Owing to their rapid degeneration, postovulatory follicles were difficult to age in laboratory specimens sampled 48 h after spawning. At this time they may be confused with intermediate stages of atretic oocytes (Lambert 1970). On the other hand, classification of postovulatory follicles into age 0 day and age 1 day was done with an accuracy of 76 to 84% (Table 1). In view of this, the following system was established for classification of ovaries from field-caught specimens:

Hydrated: ovaries with many hydrated eggs (eggs enlarged by fluid uptake just prior to ovulation) and no postovulatory follicles. (Spawning considered to be imminent.)

Age 0 day: new postovulatory follicles, showing no sign of degeneration as described above (Figure 2A, B). Hydrated eggs may occasionally be present. Elapsed time from spawning <24 h.

Age 1 day: regressing postovulatory follicles, showing degeneration as described for specimens (Figure 2C, D) sampled 24 h after spawning. Elapsed time from spawning ≥24 h but <48 h.

Nonspawning (mature): ovaries with many yolked oocytes; may contain postovulatory follicles in advanced stages of degeneration which cannot be readily distinguished from other atretic structures. Elapsed time from spawning 48 or more hours.

Immature: few or no yolked oocytes.

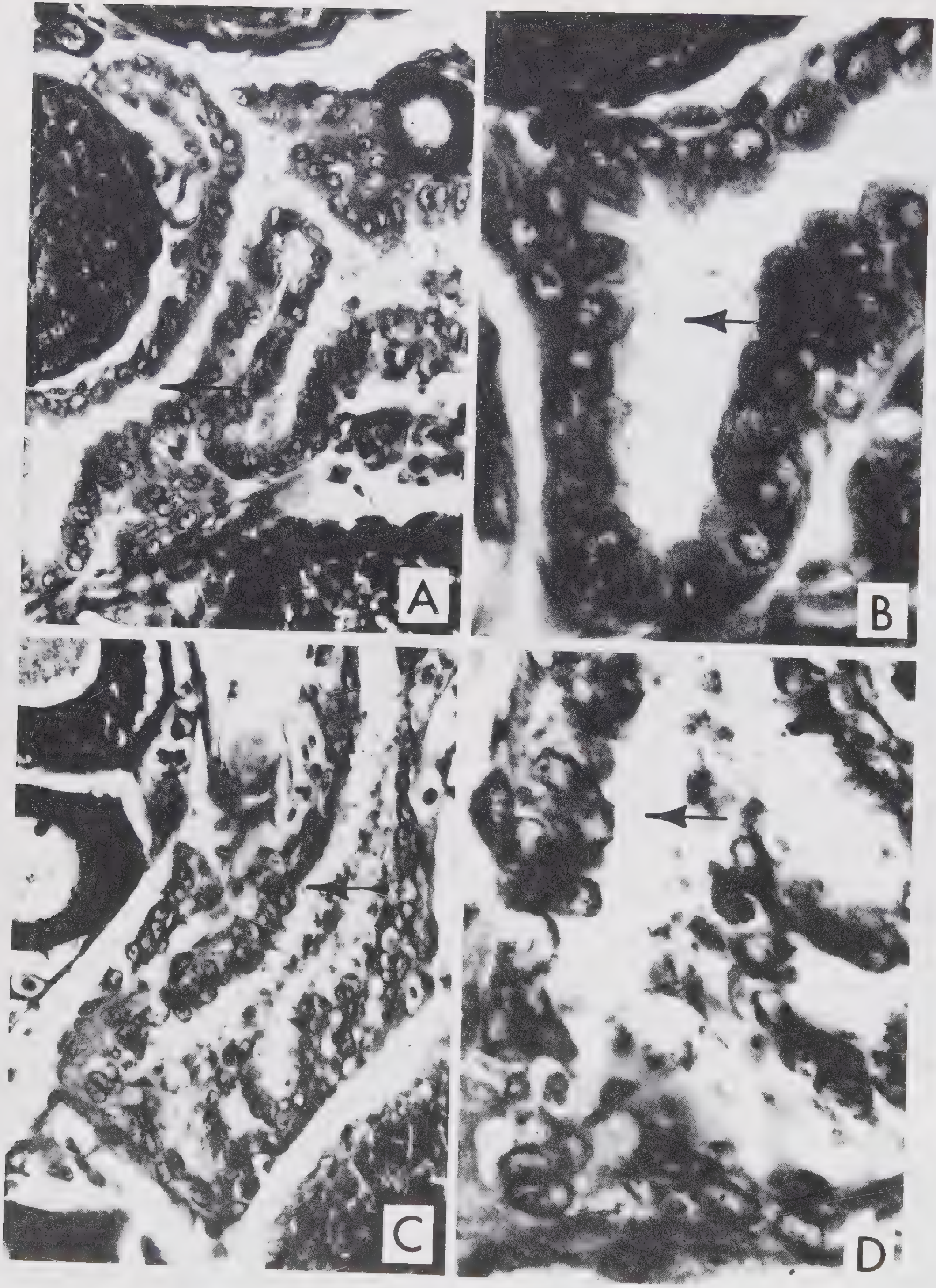

FIGURE 2.—Photomicrographs of northern anchovy ovaries from laboratory specimens: A (400×) and B (1,000×), postovulatory follicles (elapsed time from spawning 0-6 h); C (400×) and D (1,000×), postovulatory follicles (elapsed time from spawning 24 h). Arrow indicates lumen of postovulatory follicle.

TABLE 1.—Results of blind classification[1] (number of females) of postovulatory follicles of female northern anchovy spawned in the laboratory.

		Classification			
		Postovulatory follicles			
Elapsed time from spawning (days)	*n*	0 day	1 day	Postovulatory follicles older than 2 days or no evidence of spawning	Percent correctly classified
0	21	16	5	0	76
1	19	0	16	3	84
2	23	0	0	23	100
3	20	0	0	20	100
4-9	38	0	0	38	100

[1]Elapsed time from spawning was unknown to classifier.

All sea samples were classed into the above categories. The mean incidence for each category was calculated without regard to the classification uncertainties reported in Table 1. Confidence intervals for mean incidence for each reproductive state were calculated for the February set of samples but not for those taken in March or September because these sets contained only three or four samples. The normal approximation of the binomial distribution was used to estimate the confidence interval (C.I.) for the mean incidence of day 1 postovulatory follicles (95% C.I., Table 2). A normal-log negative binomial distribution (Johnson and Kotz 1970; Zweifel[7]) was used to estimate confidence intervals for the mean incidence of hydrated eggs and new postovulatory follicles because it gave a better fit to the data distribution than did the binomial distribution (Figure 3).

RESULTS

Sexual Maturity

All females taken in February and March were mature, but only 67% of those taken in September were mature. No relation existed between reproductive activity and length in the females examined. Twelve females taken in February in southern inshore stations (Figure 1) were <90 mm standard length (SL), which is smaller than any of

TABLE 2.—Reproductive state[1] of female northern anchovy collected off southern California in February 1978.

				Number of females in various reproductive states				
					Postovulatory follicles			
Station number	Day of month	Time of day	Mean length (mm)	Hydrated eggs	0 day	1 day	Mature, no evidence of spawning	Total females
2	15	1822	124	0	0	2	9	11
3	15	2053	122	1	2	2	5	10
4	15	2121	116	1	1	1	7	10
5	15	2308	117	2	2	2	4	10
7	16	1908	116	4	0	0	6	10
8	16	2147	106	2	6	0	3	11
9	16	2215	114	0	2	0	8	10
10	16	2326	114	0	1	0	9	10
11	17	0044	112	0	1	1	8	10
13	17	1835	138	0	0	1	10	11
15	17	2132	134	6	0	1	3	10
21	18	2002	137	1	0	0	9	10
27	19	2100	141	0	2	4	4	10
28	19	2230	135	0	1	2	7	10
34	20	2254	138	3	0	3	4	10
37	21	2002	139	0	0	5	5	10
38	21	2117	132	0	0	3	7	10
42	22	1934	103	4	0	3	4	11
45	22	2332	80	0	2	0	8	10
48	23	1838	136	0	0	3	7	10
49	23	2005	122	1	0	1	8	10
50	23	2202	120	0	0	1	9	10
52	24	0125	117	0	0	1	9	10
55	24	1915	126	0	1	3	6	10
57	24	2224	125	2	0	0	9	11
58	25	0009	120	1	2	4	3	10
62	25	1915	116	2	1	1	6	10
72	27	0045	111	0	0	2	8	10
75	27	2112	112	2	0	1	7	10
ΣX				32	24	47	192	295
%				11	8	16	65	100
[2]95% C.I.				6-19	5-14	12-20	—	—

[1]Immature state not included in table because all females were mature.
[2]95% confidence intervals for mean percent of females in each reproductive class.

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[7]Zweifel, J. R. 1978. Confidence intervals for the mean when sampling from natural environments. Unpubl. manuscr., 10 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

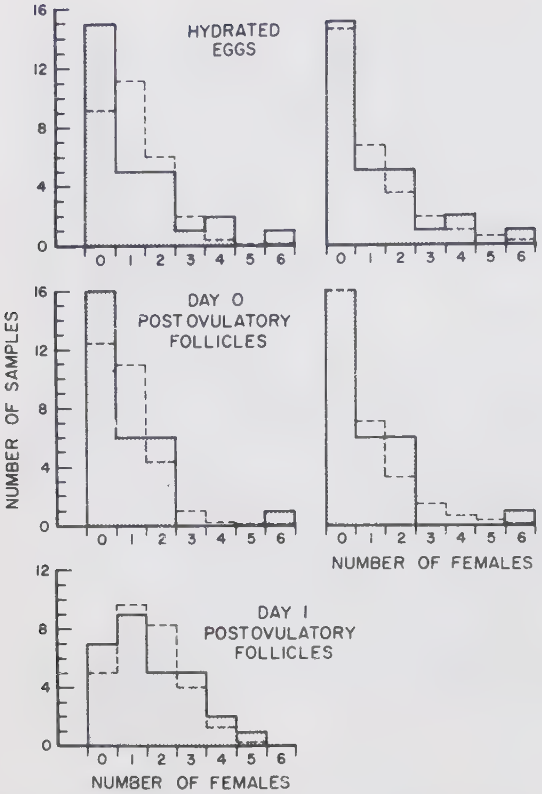

FIGURE 3.—Frequency distribution of the numbers of samples from February 1978 containing 0-6 females in each of three reproductive classes (solid bars). On left sides of the upper two panels are distributions for hydrated eggs and for day 0 postovulatory follicles, compared with that expected (dashed line) from the binomial distribution. On the right sides they are compared with that expected from the negative binomial; the negative binomial gave the better fit in both cases. Bottom panel: the frequency distribution for day 1 postovulatory follicles is compared with that expected (dashed line) from the binomial distribution, which gave an adequate fit to the data.

the reproductively active females found by Clark and Phillips (1952). They reported that only a few females mature at 90-100 mm SL, about 30% mature at 100-120 mm, and 50% at 130 mm, whereas all females we collected in February and March, regardless of size, were sexually mature. Similar to our observations, Brewer (1978) reported anchovy as small as 81 mm SL with well-developed ova from San Pedro Bay. The size of anchovy at first reproduction may have changed since 1946-52 when Clark and Phillips made their observations. On the other hand, all of our collections and those of Brewer (1978) were from southern California whereas those of Clark and Phillips (1952) included collections from the north (Monterey). It is possible that specimens living at the northern end of the range of the central subpopulation could be larger at first maturity.

Incidence of Spawning

Variation existed in the percentage of females occurring in the three reproductive states that were indicative of imminent or recent spawning. Of the females taken in February, 11% had only hydrated eggs, 8% had new postovulatory follicles, and 16% had 1-day-old postovulatory follicles (Table 2). It is critical to our objective of estimating spawning frequency to consider which of these states provided the better estimates. The distribution of the number of samples containing females with hydrated eggs and that for females with 0 day postovulatory follicles gave a poor fit to the binomial distribution indicating possible bias from contagion within samples, whereas no such problem existed for 1-day-old postovulatory follicles (Figure 3). Furthermore, evidence existed for a bias in sampling females with hydrated eggs and those with new postovulatory follicles that was related to time of day (discussed below) and with sexual composition of the school (to be discussed in a separate section). For these reasons, we believe the 1-day-old postovulatory follicles are the preferred estimator of spawning frequency.

Anchovy spawn only at night, and estimates made by Smith[8] from staged eggs indicated that most spawning occurs between 2000 and 0400 h. Since hydration precedes ovulation and spawning, one would expect the females with hydrated eggs to be the most common before 2000. In February, females with new postovulatory follicles were probably undersampled and females with hydrated eggs possibly oversampled, because most samples were taken before midnight. No females with hydrated eggs occurred in the February collections at night before 1900 h; six March females taken in the morning showed the first signs of hydration but the eggs were not sufficiently developed to be classified as hydrated. In February the number of females with hydrated eggs increased sharply after 1900 and generally remained high until 2400 (Table 3). Females with new postovulatory follicles occurred for the first

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[8] Smith, P. E. 1978. A field study of anchovy spawning time. Southwest Fish. Cent. Admin. Rep. No. LJ-78-8, 1 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 3.—Percent of female northern anchovy sampled off southern California in February 1978 with hydrated eggs, and postovulatory follicles (age 0 day and age 1 day) by time of day.

Time	Percent of females			Total no. of females
	Hydrated eggs[1]	Postovulatory follicles		
		0 day[2]	1 day	
1801-1900	0	0	19	32
1901-2000	24	5	17	41
2001-2100	6	8	24	50
2101-2200	22	14	12	51
2201-2300	10	6	12	51
2301-2400	7	17	7	30
0001-0100	3	10	23	30
0101-0200	0	0	10	10
Total				295

[1] Only hydrated eggs, no postovulatory follicles.
[2] Includes some females with hydrated eggs and new postovulatory follicles.

time between 1900 and 2000, but were more common later in the night. As expected, the occurrence of females with 1-day-old postovulatory follicles showed no pattern with time of sampling.

Despite our failure to obtain fish over the entire night of spawning, the proportion of females in February with hydrated eggs, combined with those with new postovulatory follicles, was 19% and within the confidence interval for the estimate based on 1-day-old postovulatory follicles (Table 2).

February data indicate that spawning over a 2-wk period occurred at a rate of about 16±4% of the population per night. This means that mature females spawned every 6-7 days. The three purse seine samples taken in March 1977 also indicated a high frequency of spawning; 14% of the females had 1-day-old postovulatory follicles and 9% had new postovulatory follicles (Table 4). The March collections were taken in the early morning after spawning had ended, hence the new and 1-day-old postovulatory follicles can be considered as separate estimates of spawning frequency for different days. This line of reasoning leads to the conclusion that the proportion of females spawning in March may have been about 12%, equivalent to spawning every 8 days.

Of the 24 females taken in September, only 1 had hydrated eggs, 2 had new postovulatory follicles, and none had 1-day-old postovulatory follicles. Lower spawning activity would be expected in September because egg and larval survey data indicate peak spawning usually occurs in February and March and has declined greatly by September although some spawning occurs throughout the year (Lasker and Smith 1977).

Sex Ratio and Incidence of Spawning

The sex ratio of northern anchovy schools is known to vary markedly from schools composed of nearly all females to ones composed of nearly all males (Collins 1969; Klingbeil 1978). It seemed useful to determine if spawning activity varied with sex ratio because the greatest variability in sex ratio occurs during the peak months of spawning (Klingbeil 1978). Twenty-five fish from each trawl sample taken in February 1978 were sexed. We grouped these samples into three classes on the basis of sex ratio (number of females/(males + females)) and calculated the proportion of females in each of the three sex ratio classes that fell within the following reproductive classes: spawning on the night of capture (females with hydrated eggs or new postovulatory follicles); spawning on the night before capture (females with 1-day-old postovulatory follicles); and no evidence of spawning (none of the above categories).

TABLE 4.—Reproductive state of female northern anchovy collected in March 1977 and September 1977 off southern California.

Station number	Day of month	Time of day	Mean SL (mm)	Number of females in various reproductive states					Total females
				Hydrated eggs	Postovulatory follicles		Mature, no evidence of spawning	Immature	
					0 day	1 day			
				March 1977					
1	20	0400	120	0	2	11	32	0	45
2	21	0330	119	0	7	6	54	0	67
3	21	0630	113	0	5	4	29	0	38
ΣX				0	14	21	115	0	150
%				0	9	14	78	0	
				September 1977					
1	9	2108	124	1	0	0	4	0	5
2	9	2300	129	0	2	0	9	0	11
3	10	2043	113	0	0	0	0	1	1
4	10	2236	112	0	0	0	1	6	7
ΣX				1	2	0	14	7	24
%				4	8	0	58	29	

In samples containing mostly males (mean sex ratio = 0.25), nearly 40% of the females spawned on the night of capture, whereas in samples containing mostly females (mean sex ratio = 0.84), only 10% of the females spawned on the night of capture (Table 5). A chi-square test indicated that the proportion of females spawning on the night of capture differed among the three classes of sex ratios ($P<0.001$) but no difference existed for females with 1-day-old postovulatory follicles. Therefore, most spawning occurred in male dominated schools but females that spawned on the previous night occurred in about equal proportions in all schools.

That groups of pelagic spawners could be male dominated is indicated by the reproductive behavior of another pelagic spawner, the Pacific bonito, *Sarda chiliensis*, described by Magnuson and Prescott (1966). They reported that during courtship, groups of males closely follow a single female. If male anchovy show similar behavior, then trawl collections taken at the time of spawning might be male dominated. To explain the dominance of females in commercial catches, Klingbeil (1978) suggested that male-dominated groups may not form the large dense schools necessary for effective purse seining. It seems reasonable that actively spawning (male-dominated) groups, would not be as likely to preserve the density or the integrity of the school as well as nonspawning groups. Thus, the variability in sex ratio of anchovy schools may be attributable in part to reproductive behavior, that is, the formation of male-dominated spawning groups which may be smaller and less dense than commercial schools. The female component of such groups would be expected to change from day to day because after 24 h, spawned out females occurred with equal frequency in all samples regardless of sex ratio.

Growth of Oocytes

Incidence of postovulatory follicles indicated that in February 16% of the females spawned daily or an individual female spawned on the average once every 6.25 days. In the fecundity section that follows, we show that nearly all of the eggs in the most advanced mode are spawned in one night. Thus, a new mode of eggs must mature every 6-7 days to maintain a spawning frequency of 16%. In the laboratory, spawning begins when the average diameter of the eggs in the most advanced mode is between 0.6 and 0.7 mm. Thus the eggs remaining in the ovary after spawning must attain this size in 6-7 days.

To determine if such rapid oocyte growth seemed reasonable, we estimated the mean diameter of eggs in the most advanced mode and in the second mode for some of the females taken in February and March. Females with hydrated eggs were placed in the same class as those with new postovulatory follicles because hydrated eggs were not included in this analysis. The number of females analyzed and the elapsed time from spawning were: elapsed time 0 day (hydrated eggs and new postovulatory follicles) $n = 43$; elapsed time 1 day (1-day-old postovulatory follicles) $n = 35$; and elapsed time 3.5 days (nonspawning mature females) $n = 38$. The time from spawning in the last class was unknown. We assigned the midpoint of the interval 2-5 days to this class because all fish classified as nonspawning would fall within this interval if the spawning cycle were 6 days. The mean diameter of oocytes in the second mode was estimated only for nonspawning females. In these more mature females, most of the oocytes in the second mode were >0.2 mm, whereas, in less mature fish a significant proportion of the oocytes in the second mode were <0.2 mm, and thus below the lower limit of our measurements.

The average diameter of eggs in the ovary in the most advanced mode immediately after spawning was 0.46 mm; 1 day after spawning it had increased to 0.51 mm and was 0.59 mm in nonspawning females. Figure 4 illustrates how growth in the diameter of eggs in the most advanced mode and

TABLE 5.—Sex ratio in samples (females/(males + females)) and percent of spawning northern anchovy taken in February 1978 off southern California.

Sex ratio			Percent of females			Number females classified
Sex ratio class	Class mean	Number samples[1]	Spawning on night of capture[2]	Spawned day before capture[3]	No evidence of spawning	
0.10-0.39	0.25	7	39	15	46	72
0.40-0.69	0.54	10	16	12	75	101
0.70-0.99	0.84	12	10	20	70	122

[1] Twenty-five fish per sample were used to calculate sex ratio and 10 or 11 females were examined histologically.
[2] Includes females with hydrated eggs and those with recent postovulatory follicles.
[3] Females with 1-day-old postovulatory follicles.

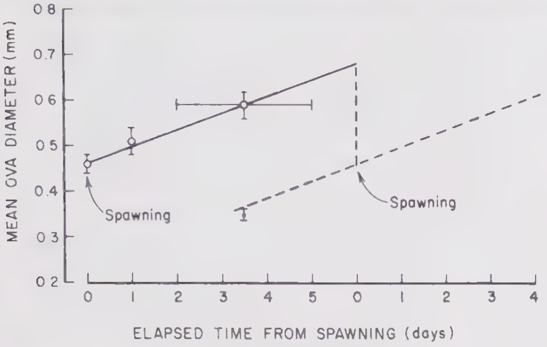

FIGURE 4.—Growth of oocytes in female northern anchovy during an assumed 6-day spawning cycle. Open circles are the mean diameter of eggs in the most advanced mode for: females with hydrated eggs (hydrated eggs excluded) combined with those with recent postovulatory follicles ("spawning"); females with day-old postovulatory follicles (second open circle): and for nonspawning females (third open circle). Horizontal bar indicates period in a 6-day cycle that females would be classified as nonspawning; and the point is plotted at the midpoint of that interval. Vertical bars are ±2 SE of mean and solid circle indicates the mean diameter of eggs in the least advanced mode for the nonspawning class.

that in the second mode could produce a 6-day spawning cycle, the second mode becoming the most advanced mode at the time of spawning. The mean diameter of the eggs in the most advanced and the second mode for the nonspawning class, when plotted at 3.5 days, seems in a reasonable position relative to the other points, indicating that the cycle may be about 6 days. A linear trajectory of oocyte growth of 0.04 mm/day indicates spawning at a diameter between 0.6 and 0.7 mm, in keeping with laboratory findings. This analysis indicates that the mean diameter of yolked oocytes of females in various reproductive stages is consistent with a 6-7 day spawning cycle.

Batch Fecundity

MacGregor (1968) estimated the number of eggs in the most advanced mode in northern anchovy ovaries to be 574 eggs/g wet weight, from an analysis of frequency distribution of eggs in 19 females. Norberg (see footnote 5) concluded that northern anchovy fecundity was 556 eggs/g, from an examination of 119 females. The supposition underlying both estimates was that the number of eggs in the most advanced mode represents the number of eggs spawned. Owing to the importance of batch fecundity in any estimate of spawning biomass from egg and larval production, we decided to reexamine spawning batch fecundity in the northern anchovy.

The assumptions underlying batch fecundity estimates are: all eggs in the most advanced mode are spawned; fecundity is directly proportional to weight; and no bias exists in the estimation of the number of eggs within the most advanced mode nor in the selection of mature females for analysis. We consider these assumptions for females taken in February 1978 using fecundity estimates for each reproductive class.

Histological examination of females with postovulatory follicles indicated that very few hydrated eggs were retained after spawning. Thus, the number of hydrated eggs within ovaries prior to ovulation (females with no postovulatory follicles) should give the most accurate estimate of the number of eggs spawned. Another advantage of using hydrated eggs was that they stand out as an isolated class, distinct from all others; they differ in appearance and are as much as 2-3 times larger than yolked oocytes. Hence, they only need to be counted; neither statistical techniques nor one's judgment need be used to separate overlapping modes.

The mean number of hydrated eggs per gram of female (ovary free) was 389±59 (±2 SE) eggs and was only 7% less than that estimated for females with the most mature ovaries (nonspawner class) (Table 6). Thus, nearly all eggs in the most advanced mode were destined to be hydrated and spawned. Fecundity estimates were substantially higher and more variable in the other three reproductive classes. Many of the females in these classes had only one mode of yolked eggs whereas about 90% of those classified as nonspawners had two modes. Fecundity estimates for the less mature females tend to be higher because the eggs destined to form a second mode have not grown sufficiently to be separated from the rest of the yolked oocytes. More variability exists because of variation among females in the extent of the differentiation of the second modal group of eggs.

In summary, we believe our most accurate estimate of batch fecundity is 389 hydrated eggs/g ovary-free female weight. If an estimate based on total female weight is needed, we recommend the one for nonspawning fish (Table 6) reduced by the fraction of eggs which may not be hydrated (7%). The adjusted fecundity for nonspawners is 368 eggs/g female weight.

Fecundity as estimated above is a function of female weight, ovary weight, and the number of

TABLE 6.—Fecundity (eggs per gram female) estimates for northern anchovy females collected in February 1978 off southern California.

		Fecundity				
		Ovary-free female weight		Total female weight		
Sample	Number of females	$\bar{x}$	SD	$\bar{x}$	SD	Percent of females with two modal groups of nonhydrated eggs
Most advanced nonhydrated eggs of females with:						
Hydrated eggs[1]	23	530	360	462	309	39
Day 0, postovulatory follicles[2]	13	693	387	497	201	69
Day 1, postovulatory follicles	19	619	313	592	294	69
None of the above (nonspawners)	33	418	186	396	171	91
Hydrated eggs	23	389	141	340	114	—
MacGregor (1968)	19	606	151	574	131	—

[1] Only the nonhydrated eggs in most advanced mode are included.
[2] Females having both hydrated eggs and postovulatory follicles were included.

advanced eggs in a weighed sample of the gonad. The number of hydrated eggs per gram of ovary did not vary with fish weight and was 2,880±373 (±2 SE) eggs/g of ovary. If any weight-related bias existed, it probably was related to the gonad weight-female weight relation. To ascertain how ovary weight varied with female weight, we separated the data into three classes on the basis of mean diameter of eggs in the most advanced mode and plotted ovary weight as a function of female weight for each class (Figure 5). The relation was slightly curvilinear; the departure from linearity was most ovbious in the 0.51-0.60 mm egg diameter class. Considering the variability in the number of mature eggs per gram of ovary, and the slight departure from linearity, no practical purpose is achieved in expressing fecundity as a function of female weight rather than as a direct proportion of weight, although direct proportionality is somewhat less accurate for extreme weight classes.

The relation between gonad weight and female weight differed somewhat among the diameter classes as can be seen in Figure 5. This might be expected because the weight of the ovary should increase somewhat with the average diameter of the eggs in the most advanced mode. We analyzed the data using multiple regression to determine if the ln (log e) gonad weight (G) could be estimated from the diameter of eggs in the most advanced mode (D), ln ovary-free female weight (W), and the interaction term (D ln G). Both female weight and the interaction term had a significant effect on gonad weight, whereas diameter alone did not. The final multiple regression equation was:

$$\ln G = -4.213 + 1.069 \ln W + 0.555 D \ln W$$

where $r^2 = 0.92$. Solving for diameter we obtain

$$D = \frac{\ln G + 4.213 - 1.069 \ln W}{0.555 \ln W}.$$

This equation may be useful for estimation of maturity stages for anchovy from weight relationships: 60% of the estimates of mean diameter were within ±0.1 mm of the observed values and the residuals were distributed evenly. The equation is more useful than gonad index (ovary weight/female weight), which is commonly employed to assess maturity, because it produces a number that can be directly related to reproduction and avoids a weight bias for extreme weight classes. The weight bias in gonad index is apparent by examination of data in Figure 5 (lowest); a 30 g female with eggs of 0.65 mm in the most advanced mode has a gonad index of 0.064 whereas that of a 10 g female at the same stage of maturity has an index of 0.040. The equation also identifies females with hydrated eggs; the average diameter of eggs estimated by the equation for females with hydrated eggs was 1.20±0.12 mm ($n = 22$) and is close to the mean of spawned eggs (1.34 mm). Obviously, such equations would be specific to populations having similar weight relations, but it does seem a useful approach for assessing maturity.

DISCUSSION

This paper provides a method for direct estimation of the frequency of spawning of a multiple spawning pelagic fish population. From such estimates it may be possible to directly estimate spawning biomass from the abundance of eggs and larvae over a short segment of the breeding season. One of the major assumptions underlying the estimate is that a representative sample of females is obtained. Spawning frequency would be overestimated if nonspawning females were in re-

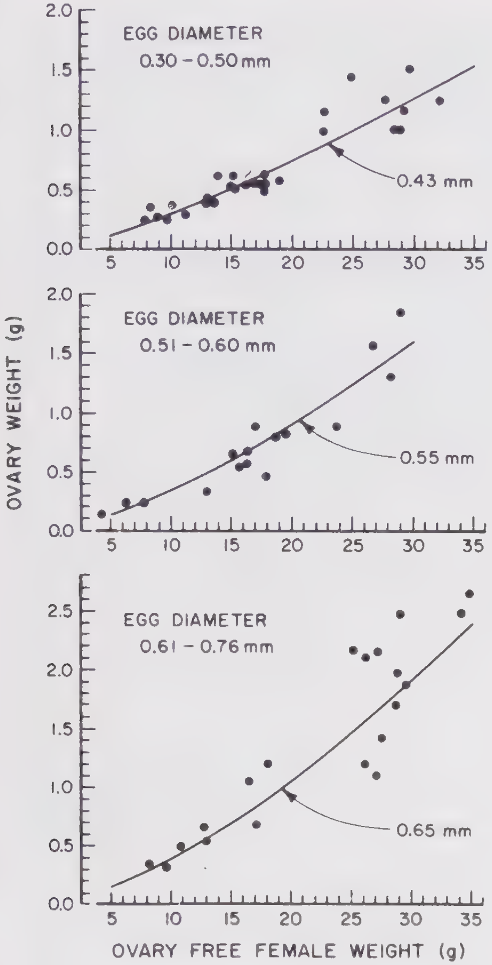

FIGURE 5.—Relation between wet weight of ovary and ovary-free wet weight of female northern anchovy classed into three groups, based on the mean diameter of eggs in the most advanced mode. Each point is a value for a single female. The lines represent multiple regressions, described in the text, for the mean egg diameters given by the arrows.

gions or at depths not sampled by the trawl or commercial purse seine. Studies need to be conducted at other times of the year and employing other sampling techniques to answer these questions.

This paper also describes a new method for estimation of batch fecundity in a multiple spawning fish. Our estimation for northern anchovy based on hydrated eggs (389 eggs/g female weight, less ovary), was substantially less than that of MacGregor (1968) (606 eggs). This difference could be attributed to annual variation in fecundity because variations of this size are known to occur in fishes (Bagenal 1973). On the other hand, our selection of females on the basis of reproductive state also may have been responsible for at least part of the difference. Our estimates for females that had recently spawned (day 0 and day 1 postovulatory follicles, Table 6) were close to MacGregor's estimate. In recently spawned females, modal groups of eggs were less distinct, and often one mode was considered to exist when the eggs may have been destined to form two spawning batches. If MacGregor (1968) used such females, this could explain in part why his estimate was higher than our estimates based on hydrated eggs or on fish classed as nonspawning. In addition, our technique of partitioning eggs occurring between two modal groups according to an assumed normal distribution may have decreased our estimate somewhat relative to past methods. Use of hydrated eggs avoids these problems, but it does require histological examination to insure that none of the females used for the estimate have begun ovulation. Apparently, some of the females we captured were spawning because their ovaries contained many new postovulatory follicles as well as many hydrated eggs. We usually examined only one set of histological sections to determination if ovulation had occurred; histological examination of an entire ovary was impractical. We believe our examination was adequate because our estimate based on hydrated eggs was close to the one based on females with the most advanced ovaries (nonspawning).

In addition to the obvious application to the estimation of spawning biomass, this work provided insights into the reproductive biology of *E. mordax*. The high spawning frequency, the ability to rapidly mature new batches of yolked oocytes, and the long breeding season of the northern anchovy (Lasker and Smith 1977), indicate that energy reserves and the availability of food may set the limit to the number of spawnings and hence to total fecundity. The analysis has also provided a possible explanation for the variability in the sex ratio of catches of anchovy.

ACKNOWLEDGMENTS

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EARLY LIFE HISTORY OF PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

The early life history of Pacific mackerel, *Scomber japonicus*, is described from laboratory-rearing studies and examination of stomach contents of sea-caught larvae. At 19° C mackerel eggs hatched in 56 hours, larvae were 3.1 mm standard length with a dry weight of 0.04 mg of which 50% was yolk. First feeding occurred 46 hours after hatching; all larvae fed by 60 hours (age 2.5 days). Larvae were then 3.6 mm long with fully pigmented eyes and 10% of the yolk remaining. Starvation was irreversible if larvae were not fed before age 4.5 days. Metamorphosis (15 mm standard length) occurred in 24 days at 16.8° C to 16 days at 22.1° C. Larvae 3-5 days old consumed 87% of their body weight per day and had a mean gross growth efficiency in dry weight of 33%. Oxygen consumption was 6.1 μl O_2 per milligram dry weight per hour at 18° C and 11.4 μl O_2 per milligram dry weight per hour at 22° C. Swimming speeds ranged from 1.3 standard lengths per second for first-feeding larvae to 3.8 standard lengths per second for fish at metamorphosis. Fifty percent of the larvae were able to capture a prey when the width of the prey was 85% of the width of the mouth and 95% were able to do so when the prey was 57% of the width of the mouth. Cannibalism was common in rearing groups; at 8 mm standard length, 50% of the larvae became capable of feeding on other fish larvae and cannibalism ceased when schooling commenced. Chief food items of sea-caught larvae were stages of copepods; maximum food width increased rapidly with larval length and was equivalent to the maximum mouth width. Mean prey width was 38% of mouth width. The larger organisms, constituting half of the prey eaten, accounted for 85-90% of the total volume of food eaten.

The development and distribution of eggs and larvae of the western Pacific population of the Pacific mackerel, *Scomber japonicus*, has been described (Kramer 1960; Kramer and Smith 1970), but little information exists on growth, behavior, and physiology of the larval stages. Incubation times and other data are known for the Japanese population of *S. japonicus* (Watanabe 1970). This paper provides some of the information needed to characterize the early life history of Pacific mackerel, including incubation times, yolk absorption, onset of feeding, vulnerability to starvation, swimming and feeding behavior, food ration, and oxygen consumption.

METHODS

Laboratory Experiments and Sea Samples

Eggs were obtained from Pacific mackerel maintained in spawning condition in the laboratory and induced to spawn by hormone injection (Leong 1977). Effects of temperature on incubation time were determined by placing test tubes containing 10 eggs and 25 ml of seawater in a temperature block set to produce a temperature gradient of 11.1°-23.3°±0.2° C (2 SE (standard error)) (Lasker 1964). Hatched eggs were counted at 2-4 h intervals and time from fertilization to 50% hatch estimated. Rate of yolk absorption was determined at 19.4°±0.4° C by measuring the surface areas of the yolk-sac and oil droplet from tracings made with an optical comparator (Wolfson 1965). Six samples, each of 15-25, larvae were taken over the first 72 h after hatching.

To estimate the time of first feeding at 18.9°±0.3° C, groups of larvae without past feeding experience were transferred to a 100 l container containing 150 rotifers/ml (*Brachionus plicatilus*). Four hours later, they were removed and the percentage of larvae that fed and the mean number of rotifers in the gut were calculated. Eight groups of 10-39 larvae were tested at periods from 18 to 114 h after hatching.

A starvation-based mortality curve was establised at 19.0°±0.3° C by starting with 1,000 eggs in each of two 200 l containers, and counting and removing dead larvae daily. The age was determined at which starvation became irreversible in first-feeding larvae. Seven hundred and fifty eggs were incubated in each of four 200 l tanks and the resulting larvae were fed for the first time at

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ages 2.5, 3.5, 4.5, and 5.5 d. The percentage survival was determined on the eighth day. Larvae were fed rotifers (50/ml) on the first day of feeding, and rotifers and copepods (*Tisbe* sp.) thereafter.

Vulnerability of newly metamorphosed Pacific mackerel (mean length 16.7 mm SL (standard length)) to starvation was tested at 18.9°±0.2° C by transferring fish from the rearing container to containers without food. One group of fish was starved for 4 d, another for 5 d, and a third was fed *Artemia salina* nauplii. The two starved groups were fed at the end of the starvation period.

Tail beat frequency and amplitude of larval Pacific mackerel (3-5 mm SL) were determined for routine swimming and burst speeds by analysis of cine films taken at 100 frames/s using techniques described by Hunter (1972). Routine swimming speeds of larval mackerel, at 19° C, were measured by counting the number of squares crossed by a larva (3.7-6.6 mm SL) as it swam over a 1 cm grid on the bottom of the rearing tank for 9-153 s; a 3 cm grid was used for larger larvae (7.9-13.1 mm SL) with shorter observation times (3-46 s). The mean of 15-25 visual observations was used as an estimate of speed for the mean length of the larvae in the tank on the day of observation; speeds were adjusted for parallax caused by the difference in depth between the grid and the fish. Speeds of juveniles (>19 mm SL) were measured by timing the fish as they swam a measured distance (35-201 cm) around the perimeter of the rearing tank; in this case mean speeds were for individual fish and observation times ranged from 3 to 26 s.

The size at which Pacific mackerel larvae were capable of ingesting various prey was evaluated by placing them in a 110 l container with the prey and estimating the number that fed by examination of stomach contents. The type of prey, mean prey size, prey density, and duration of feeding respectively were: yolk-sac anchovy larvae, 2.7 mm SL, 8/l, 2 h; *A. salina* nauplii, 0.2 mm wide, 11/l, 4 h; and anchovy eggs, 0.67 mm wide, 10/l, 2 h. The mouth width, prey width, and standard length of the larvae were measured and percentage feeding success was estimated for size classes of larval length and mouth width. The number of fish per size class was >9. Size thresholds for 50% feeding success and 95% success were estimated by probit analysis (Finney 1952) and expressed as a function of mean larval length, or mean prey width/mean mouth width.

The sizes of food items eaten by Pacific mackerel larvae in the sea was determined by examination of the stomachs of 86 larvae taken in routine ichthyoplankton surveys along the California coast. We recorded the length of each larva and the number and maximum width of all identifiable food items (Arthur 1976; Shirota 1970).

Food requirements were estimated by feeding the rotifer *Brachionus plicatilis* to 3-5 d old Pacific mackerel larvae. Seven to eight samples of 9-16 larvae each were taken over each of three 12-h feeding days, the number of rotifers in the guts of each larva were counted, and the counts converted to equivalent dry weight using the conversion factor of 0.16 μg/rotifer (Theilacker and McMaster 1971). Daily changes in larval weight were estimated from mean standard lengths using a length-dry weight conversion given in the results. The rate of gastric evacuation for 4 mm SL larvae was measured. They were allowed to feed for 4 h and then transferred to a tank without food; samples of 13-16 larvae were taken at about hourly intervals until the stomachs were empty. The number of rotifers in stomachs were counted and converted to dry weight, and the rate of gastric evacuation was estimated in terms of dry weight. The daily ration was estimated from the mean stomach contents and the rate of gastric evacuation. Gross growth efficiency was estimated in terms of dry weight from the daily ration and weight gain over 24 h.

Metabolic requirements of Pacific mackerel larvae were estimated using a Warburg respirometer and standard manometric techniques (Umbreit et al. 1964) to measure oxygen consumption. One or more Pacific mackerel larvae were added to an 18 ml Warburg flask filled with 4.4-8.7 ml of filtered seawater (salinity 33.58-33.93‰). Larvae >0.06 mg dry weight were tested individually. Twenty-one tests were made at 18.0°C of larvae or groups of larvae ranging in length from 3.7 to 17.9 mm SL (0.038-12.74 mg) and 14 at 22.0° C, of larvae 3.2-10.5 mm SL (0.025-2.86 mg). Flasks were shaken at 102 times/min for 5 out of every 30 min; readings were taken after the first 2 h and continued for 150-360 min. At the end of a test, larvae in each flask were measured, rinsed in distilled water, oven dried to a constant weight, and weighed. Mean weight was obtained for fish tested in groups. All runs were made under normal room illumination, about 700 lx. $\log_{10}$ oxygen consumption in microliters O_2 per hour was regressed on $\log_{10}$ body weight for the 18.0° and 22.0° C experiments. As the slopes were close to unity, oxygen consumption was expressed in microliters per milligram per hour. Metabolic requirements were compared with daily ration by converting oxygen consumption and daily ration to calories (1 μl O_2 = 0.005 cal: one *Brachionus plicatilis* = 0.00085 cal, Theilacker and McMaster 1971).

Culture of Larvae

Seven groups of Pacific mackerel were reared to metamorphosis to determine growth rates and effects of temperature on growth. The rearing containers were black fiber glass, cylindrical tanks (122 cm in diameter × 36 cm deep). Culture volume increased during the rearing period from 200 to 400 l because of the addition of seawater containing food and algae. Tank temperature was controlled by a regulated water bath, and groups were reared at temperatures ranging from 16.8° to 22.1° C. Illumination at the water surface during the 12-h day was about 2,000 lx. Tanks were started with 3,000 eggs/group. Initially, larvae were fed laboratory-cultured *Brachionus plicatilis*. At age 5 d, laboratory-cultured copepodids and adult copepods (*Tisbe* sp.) were added; 200,000 copepods were added daily until metamorphosis. Initially 30 or more rotifers/ml were added for the first few days of feeding; thereafter the density of rotifers was allowed to decline. On a diet of rotifers alone, growth slowed after larvae reached 5 mm SL and few larvae survived longer than 15 d. Newly metamorphosed juveniles were fed live and frozen adult *A. salina* and minced squid (*Loligo opalescens*) and northern anchovy. From 1 to 6 l of algal culture, *Tetraselmis* sp. (300,000-500,000 cells/ml), were added daily to provide food for rotifers and copepods. Samples of 10 or more larvae were taken on alternate days for length measurements. Some samples were washed in distilled water, dried, and subsequently weighed to obtain a relation between length and dry weight.

RESULTS

Hatching, Onset of Feeding and Starvation

Eggs of Pacific mackerel are transparent spheres, ranging in diameter from 1.06 to 1.14 mm (Kramer 1960). Incubation times ranged from 33 h at 23° C to 117 h at 14° C (Figure 1); eggs did not hatch below 14° C. The curve for hatching time as a function of temperature for the western Pacific population (data from Watanabe 1970) appears to be the same as the one for the eastern Pacific population.

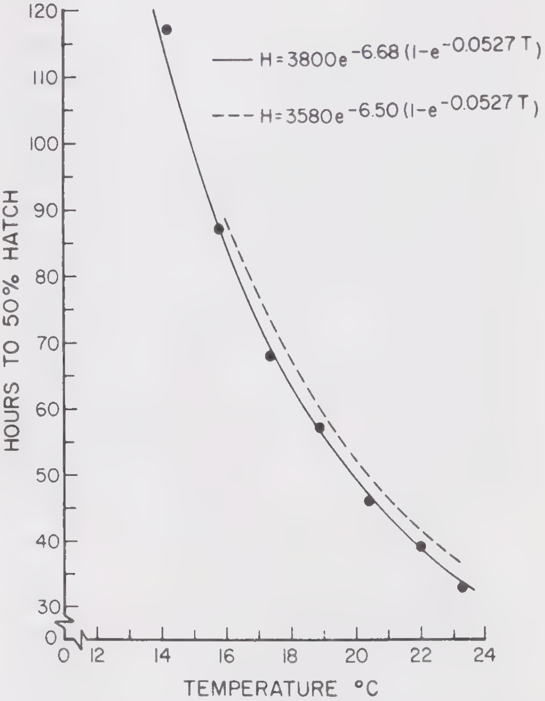

FIGURE 1.—Incubation time (fertilization to 50% hatch) of *Scomber japonicus* eggs. Solid line is for present data, points are estimated time to 50% hatch of eggs in five test tubes per temperature, dashed line is for data of Watanabe (1970). The general equation was developed by Zweifel and Lasker (1976) and fit to the 50% values.

At hatching, larvae averaged 3.1 mm SL (Figure 2B) and weighed 0.040 mg dry weight, of which 50% was yolk. At 19° C, first feeding occurred 46 h after hatching; by 60 h after hatching, all larvae had ingested one or more rotifers in 4 h (Figure 2D). Thus the 50% threshold for onset of feeding at 19° C occurred at about 50 h (2 d) after hatching. At this time larvae were 3.6 mm SL, the eyes were fully pigmented and 10% of the yolk remained, principally the remnants of the oil droplet (Figure 2A, B). Over the threshold for the onset of feeding, the mean number of rotifers in Pacific mackerel stomachs increased from 2 at 46 h to 14 at 68 h (Figure 2E). The larvae in each group had no previous feeding exposure, hence the increase in feeding activity with time could not be attributed to experience.

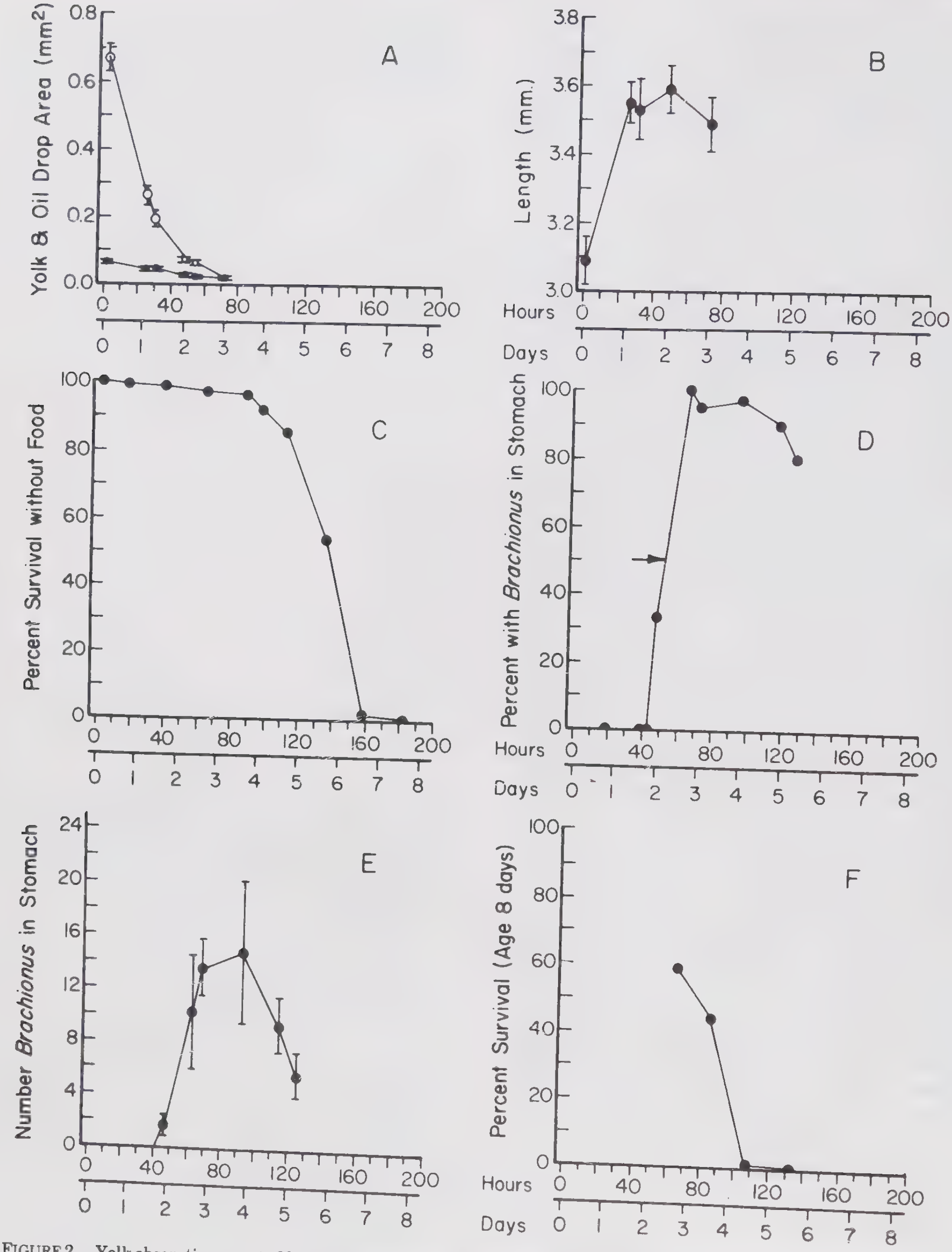

FIGURE 2.—Yolk absorption, onset of feeding, starvation, and point of irreversible starvation in Pacific mackerel larvae at 19° C: A. Rate of yolk absorption—open circles mean area of yolk-sac, solid circles mean area of oil droplet (mm²). B. Mean length of larvae from hatching through yolk-absorption. C. Percent survival of larvae without food. D. Percent of larvae tested at various times after hatching that had ingested one or more *Brachionus plicatilis* in a 4-h test period—arrow indicates the 50% threshold for the onset of first feeding. E. Mean number of *B. plicatilis* per positive stomach of larvae tested at various times after hatching. F. Percentage survival at age 8 d for larvae fed for the first time at age 2.5, 3.5, 4.5, and 5.5 d—percentages are plotted at the time food was first added. Bars in A, B, and E represent ±2 SE of mean.

If larvae were not fed, most died between ages 4 and 7 d and none survived longer than 7 d (Figure 2C). Highest survival (on the eighth day after hatching) occurred when food was added for the first time at age 2.5 d; survival was somewhat lower if food was added at 3.5 d and negligible if added at 4.5 d (Figure 2F). Thus at 19° C starvation appeared irreversible if food was not provided before 4.5 d.

Pacific mackerel larvae, unlike herring or anchovy (Blaxter and Hempel 1963; Lasker et al. 1970), did not cease swimming or feeding at the time of irreversible starvation. At age 5 d, the incidence of larvae with rotifers in their stomachs was relatively high (80%) (Figure 2D), but the average number of rotifers per positive stomach was much less than in larvae fed first at age 2 or 3 d (Figure 2E). Thus at age 5 d, most larvae were still able to feed, but owing to their weakened condition, none were able to capture enough prey to survive.

Vulnerability of larvae to starvation persisted through metamorphosis. All juvenile Pacific mackerel appeared emaciated and swam slowly by the fourth day of starvation. Mortality of 10% occurred in the group starved 4 d; 50% mortality occurred in those fish starved 5 d. All juveniles surviving 4 and 5 d of starvation recovered when food was added; no mortality occurred in the controls. Thus, newly metamorphosed Pacific mackerel were able to withstand 1 or 2 d more of starvation than first-feeding larvae, but they were better able to recover from food deprivation.

Growth

Growth in length of Pacific mackerel larvae was slow and almost linear over the first 10-15 d until larvae reached about 6-7 mm SL; there followed a rapid acceleration through metamorphosis. We did not fit equations to these data because none of the standard growth equations gave a good fit to the entire growth curve. The effect of temperature on growth was not distinguishable over the initial growth period, but became obvious during the period of rapid growth (Figure 3, Table 1). To provide an index of the effect of temperature on growth, we expressed the duration of the larvae period (hatching to metamorphosis, 15 mm) as a function of temperature (inset in Figure 3). The Q_{10} was 3.0 when calculated from the equation in Figure 3 for the temperature range of our observations (16.8°-22.1° C).

The length-weight relation for Pacific mackerel larvae and juveniles is shown in Figure 4. The form of this equation was developed by James Zweifel and used by Hunter (1976) to express the length-weight relation for northern anchovy larvae. The curvilinear nature of the length-weight relation, still evident in the log-log plot (Figure 4), indicates that if a linear regression of $\log_{10}$ weight

TABLE 1.—Growth data (millimeters SL) for seven groups of *Scomber japonicus* larvae reared at different mean temperatures from hatching through metamorphosis.

Age (days)	22.1° C[1]			20.4° C			19.6° C			19.5° C			19.2° C			18.9° C			16.8° C		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
1										10	3.1	0.24							31	3.5	0.12
2	14	3.3	0.21	16	3.8	0.06	16	3.7	0.10	15	3.9	0.09	15	3.8	0.06						
3	14	3.5	0.30																		
4	10	3.6	0.22	18	3.8	0.26	33	4.2	0.23	10	4.0	0.17	15	4.0	0.20	10	3.7	0.20			
5																					
6	10	3.9	0.21	15	4.2	0.41	15	4.8	0.44	13	4.2	0.14	15	4.4	0.37	10	4.1	0.39	15	4.3	0.42
7										27	4.5	0.40									
8	12	4.5	0.55	15	5.7	0.77	15	6.0	0.39	25	4.7	0.56	15	5.0	0.40				15	5.1	0.43
9													5	5.9	0.13						
10	12	6.0	1.13	15	6.3	0.91	15	6.6	0.70	15	4.8	0.43	19	5.6	0.77	11	5.2	0.45			
11																			15	6.5	0.70
12	22	8.4	1.88	16	8.2	1.31	15	6.5	0.75	11	5.9	1.08	25	6.4	0.68	12	6.1	0.60	15	7.0	0.50
13																					
14	10	8.9	1.46	10	11.5	1.54	15	8.4	1.12	30	6.4	1.09	15	6.6	0.80				17	7.7	1.40
15																			11	8.1	1.08
16	10	14.9	1.45	15	14.1	2.01	15	8.9	1.76	16	8.5	2.21	15	7.1	0.81	13	7.6	1.50			
17										10	10.0	2.71				12	9.0	1.33	15	10.3	2.11
18				15	17.8	1.70	15	10.3	2.48				15	10.3	3.21	13	9.4	1.61	17	10.8	2.84
19	15	24.1	5.81																		
20							15	12.5	3.18	17	17.7	4.21	15	11.7	2.88				9	11.5	2.81
22							15	17.5	4.51				15	14.6	4.62						
23																15	13.7	1.26			
24							24	20.4	5.10				16	18.5	5.38	10	19.8	2.36			
25																			17	17.1	5.07

[1] Juvenile growth (age, *n*, $\bar{x}$, and (SD)): 26 d, 13, 34.4 mm (4.37); 29 d, 9, 43.9 mm (3.60); 39 d, 5, 55.0 mm (8.74); and 47 d, 9, 67.3 mm (10.30).

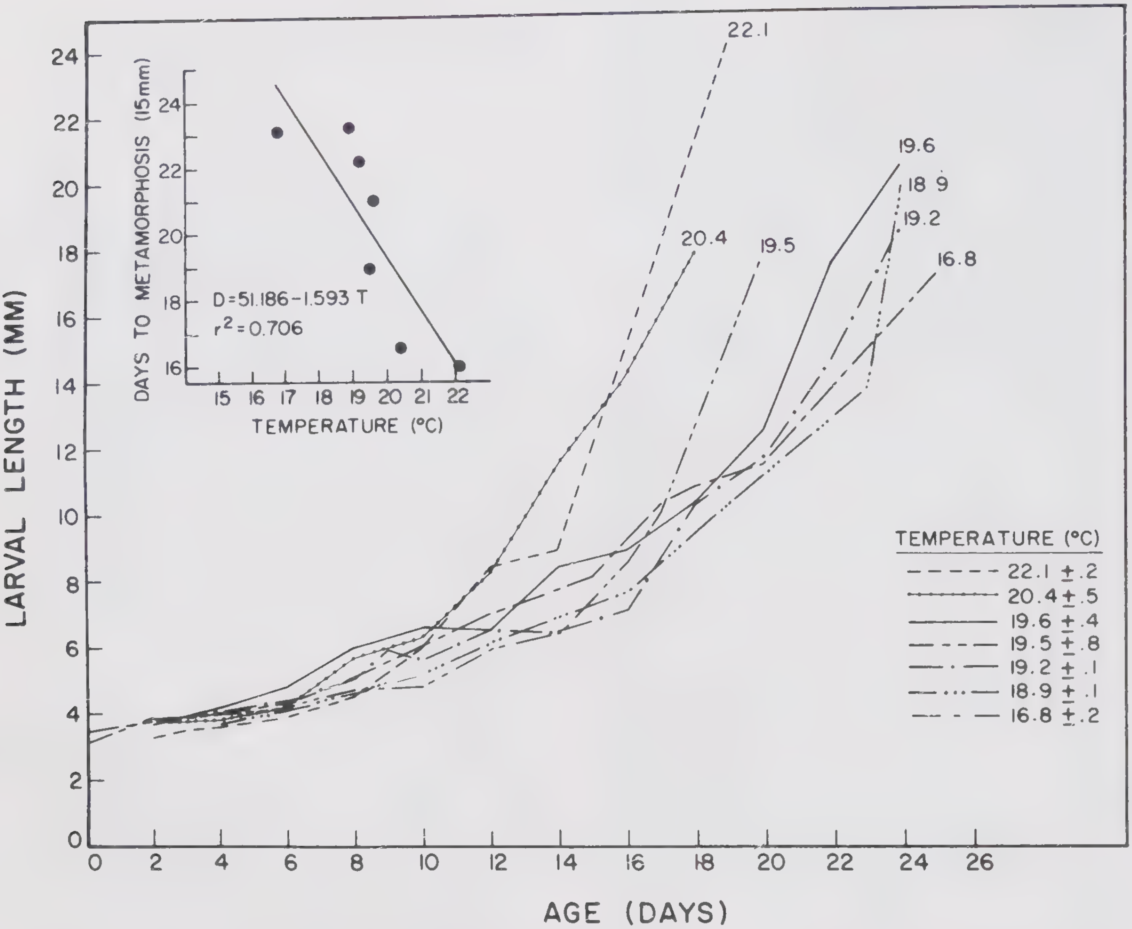

FIGURE 3.—Growth of seven groups of Pacific mackerel larvae reared in the laboratory from hatching (age 0 d) through metamorphosis (15 mm SL). Lines connect means given in Table 1; rearing temperatures (±2 SE) given on right side of figure and at end of lines. Inset at top: elapsed time (days) from hatching to metamorphosis (15 mm), as a function of rearing temperature.

on $\log_{10}$ length were used, it would produce inaccurate estimates.

Swimming Behavior

At typical cruising speeds, larval Pacific mackerel (3-5 mm SL) have a high tail beat frequency of about 30 beats/s and a low tail beat amplitude of 0.16 standard length. At slow speeds, tail beat frequency remained relatively constant but the amplitude of the tail beat changed. At higher speeds, both amplitude and frequency changed but the relative increase in amplitude was much greater than that of frequency (Table 2). Thus larval Pacific mackerel, unlike the adults (Hunter and Zweifel 1971), predominantly modulate tail beat amplitude to effect changes in speed.

Cruising speeds of Pacific mackerel increased markedly over the larval period from 0.46 cm/s (1.3 standard body lengths/s) for first-feeding larvae (3.6 mm SL) to 5.6 cm/s (3.8 standard body lengths/s) for fish at metamorphosis (Figure 5). This differs from the pattern in adult fishes where speed relative to size decreases with an increase in fish size (Webb 1975).

Feeding Behavior

Upon sighting a prey (rotifer or copepod), a Pacific mackerel larva advanced toward the prey,

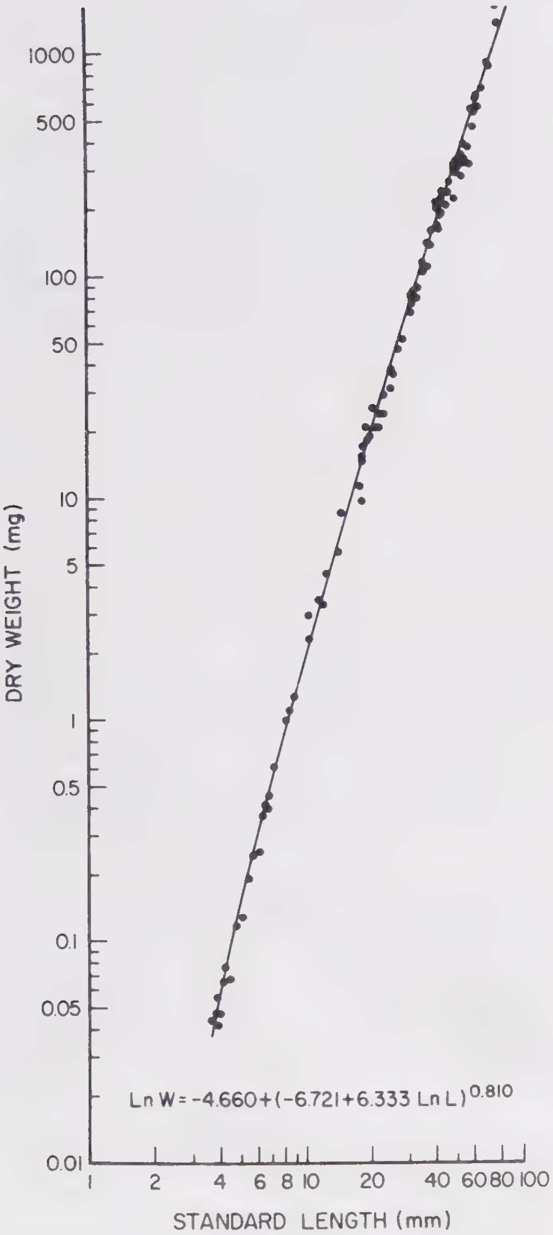

FIGURE 4.—Relation between dry weight (W) of larval and juvenile Pacific mackerel in milligrams and standard length (L) in millimeters. Points are observed values for individuals >18 mm and for larvae <18 mm; points are means for groups of 15 larvae.

stopped, drew back the tail, and held it in a slightly recurved, high amplitude position while the rest of the body remained relatively straight.

mm larval Pacific mackerel ($\bar{x}$ = 4.23 ± 0.09 mm SL) expressed as a function of standard length.

			Tail beat	
N	Swimming speed (SL/s) Class interval	Mean	Frequency (beats/s)	Amplitude/SL
18	0.01- 1.0	0.58	33.2	0.12
30	1.01- 2.0	1.48	30.2	0.16
9	2.01- 3.0	2.48	30.2	0.17
3	3.1 - 5.0	4.00	37.5	0.18
3	10.1 -15.0	12.18	39.4	0.29
1	—	37.04	38.9	0.33

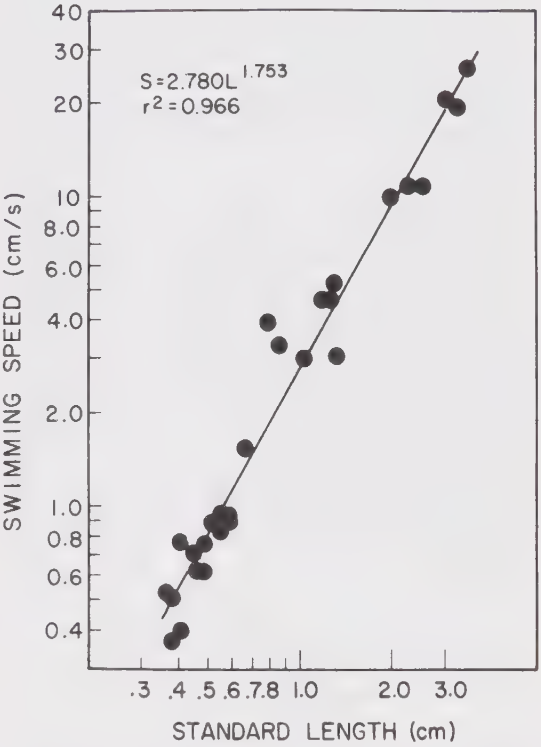

FIGURE 5.—Relation between swimming speed and standard length of Pacific mackerel larvae ($\log_{10}$ scales) at 19° C. Each point <2.0 cm is the mean of 15-25 observations. For ≥2.0 cm, individual fish were measured.

Feeding involved driving the tail posteriorly and opening the mouth. Larvae often attacked the same prey two or more times if the previous strike was unsuccessful, and repositioned for subsequent strikes by moving backward. Handling times were negligible because the prey was engulfed instantaneously. Older Pacific mackerel larvae developed a set of motor patterns for feeding on fish larvae; larvae were seized from the side and carried crosswise in the mouth. Larger prey were repeatedly released and grasped until they ceased struggling, then released and ingested, usually head first. Handling times increased with prey size.

The length at which 50% of Pacific mackerel larvae were capable of capturing and ingesting anchovy yolk-sac larvae (LD_{50}, Finney 1952) was 8.1 mm SL (95% confidence interval, 7.2-9.5 mm) (Figure 6). Sibling cannibalism began when the mean length of the group was about 8 mm SL. At this size, the mean length of six cannibals was 10.8 mm SL (range 9.9-12.0 mm) and that of their prey was 6.2 mm SL (range 5.9-6.5 mm). Cannibalism in rearing containers ended as Pacific mackerel approached metamorphosis (15 mm SL) and schooling began. Rearing at higher temperatures increased the growth rate and thereby decreased the period over which sibling cannibalism occurred. Consequently, survival at metamorphosis was higher in groups reared at 20°-22° C (5-6%) than it was at 19° C or lower temperatures (1-2%).

Near metamorphosis, Pacific mackerel were able to eat relatively large fish larvae. Three Pacific mackerel, 15.4-16.0 mm SL, placed in a rearing tank with northern anchovy larvae (12.0-20.6 mm SL) captured and began to ingest larvae of 11.7-13.5 mm SL, within 6 min. Thus, as Pacific mackerel larvae grew from 8 mm SL to metamorphosis, the size of anchovy larvae, they were able to eat increased from about 3 to 13 mm SL. This increase in prey size was not closely related to mouth size of the Pacific mackerel because the mouth can be greatly expanded when ingesting a larval fish. Mouth size probably was inversely related to handling time as in the case for adult fishes (Kislalioglu and Gibson 1976).

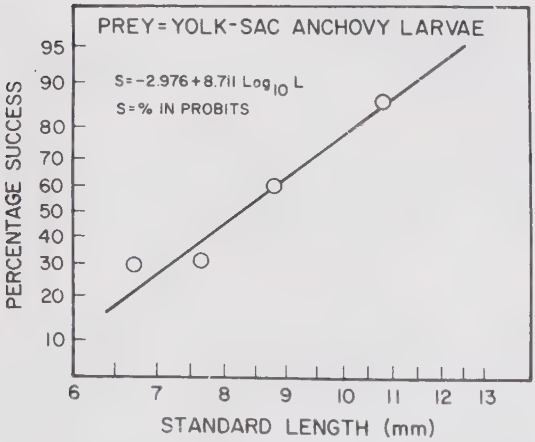

FIGURE 6.—Percentage of Pacific mackerel larvae (probit scale) that captured one or more yolk-sac anchovy larvae in relation to standard length of the mackerel ($\log_{10}$ scale). The length class was variable. Larvae were ranked by length and classes set at 10 observation intervals. The LD_{50} was 8.1 mm (95% confidence interval 7.2-9.5 mm).

When prey are engulfed rather than seized, mouth size may give a good indication of the size of prey a larvae is capable of ingesting. The relation between mouth width and length in Pacific mackerel larvae was slightly curvilinear, and mouth width increased from 0.216 mm for first-feeding larvae (3.6 mm SL) to 0.987 mm at metamorphosis (15 mm SL) (Figure 7).

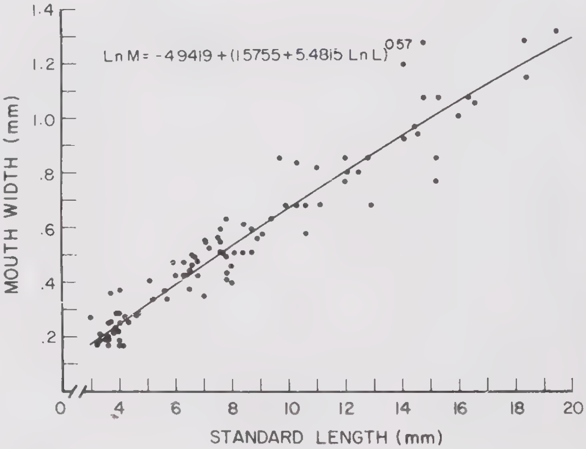

FIGURE 7.—Mouth width as a function of standard length of Pacific mackerel larvae. Points represent single larva.

The threshold, in terms of length for feeding on *A. salina* nauplii, was distinctly different from that for feeding on anchovy eggs. The 50% threshold for nauplii was 4.5 mm SL (95% confidence interval, 4.1-4.8 mm) and that for eggs was 12.2 mm SL (11.3-13.1 mm). This could be expected because anchovy eggs are nearly three times as large as *A. salina* nauplii. On the other hand, when feeding success was expressed as a function of the ratio, mean prey width/mean mouth width, the percentage feeding success of Pacific mackerel fed *A. salina* was similar to that of larvae fed eggs (Figure 8). At first feeding, relative prey size (prey width/mouth width) was near unity for larvae fed either *A. salina* or eggs, indicating the width of the mouth established the upper size limit of prey. Since the 50% threshold for relative prey size for the combined data given in Figure 8 was 0.85 (95% confidence interval,

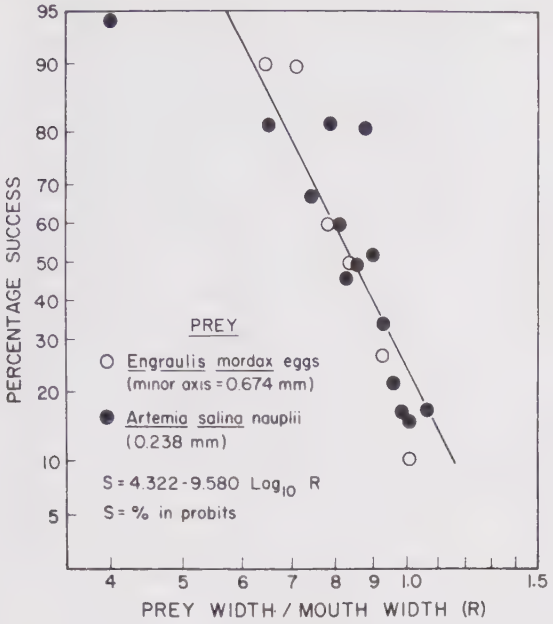

FIGURE 8.—Relation between average feeding success (probit scale) and average relative prey size (prey width/mouth width), for larval groups fed *Artemia salina* nauplii (closed circles) and northern anchovy eggs (open circles). Each point is the percentage success of fish within a mouth width/prey size class, where $n>9$. Line is the regression of percentage success probit on $\log_{10}$ of the prey-width to mouth-width ratio, for *A. salina* nauplii and anchovy egg data combined. The LD_{50} for the combined data was 0.85 (95% confidence interval 0.79-0.91).

0.79-0.91) and the 95% threshhold was 0.57 (0.47-0.70), nearly all Pacific mackerel larvae (95%) were able to ingest a prey when it was 57% of the width of the mouth and 50% were able to do so when it was 85% of the mouth width.

Nearly all prey eaten by Pacific mackerel larvae in the sea fell within the range of sizes predicted from the laboratory work; few prey exceeded the width of the mouth (Figure 9). Fifty-nine percent of all identifiable food items in the stomachs of sea-caught larvae were stages of copepods; other items included cladocerans, oikopleurans, gastropods, invertebrate eggs, diatoms, fecal pellets, and one fish larvae.

Although laboratory data indicated that 50% of Pacific mackerel larvae were able to ingest prey having a width of 85% of the mouth width, the mean diameter of prey eaten in the sea was 38±2% (2 SE) of the mouth width. Thus, a substantial number of prey eaten by larvae in the sea was much smaller than the maximum size of prey they were capable of ingesting. This may reflect a shortage of larger prey in the sea. Larger prey probably are important nutritionally. If one assumes the prey given in Figure 8 to be spherical, then 50% of the prey items accounted for about 85-90% of the total volume of food, depending on larval size. Conversely, the small prey items that contributed 50% by number, contributed only 10-15% of the total volume of prey eaten. This calculation underestimates the volume of the larger prey because they are more elongate or less spherical than smaller ones. Nevertheless, it indicates that prey less than the mean size eaten contributed relatively little nutritionally to the diet of Pacific mackerel larvae, and that the relatively large, but more rare, prey probably made the major contribution to growth.

Ration, Growth Efficiency and Metabolism

Pacific mackerel larvae (age 3-5 d) fed actively throughout the day; the gut was filled within the first hour of feeding and it remained full throughout the remainder of the 12-h feeding day, despite a high rate of gastric evacuation. Evacuated *Brachionus plicatilis* were well digested; only the lorica remained after digestion. Our measurements of evacuation rates indicated that about half the gut contents was evacuated in 2 h (Figure 10). Growth of larvae used for ration estimates was about the same as that for other groups reared at 19° C (Figure 3). To grow at this rate in the laboratory, Pacific mackerel larvae (age 3-5 d) consumed an average of about 87% of their dry body weight per day, or about 165-538 rotifers/day (Table 3). This estimate of ration was based on the dry weight of the mean number of rotifers in stomachs, adjusted for the rate of evacuation (Stauffer 1973). The mean gross growth efficiency in dry weight was 33%, which falls within the range of estimates for fish larvae and young fishes (Pandian 1967; Stepien 1976).

Our respiration experiments indicated that Pacific mackerel larvae at 18.0° C consumed 6.1±1.4 (2 SE) $\mu l\ O_2$/mg per h ($n = 24$) and at 22.0° C they consumed 11.4±3.0 $\mu l\ O_2$/mg per h ($n = 14$). By interpolation, the rate at 19° C, the temperature of the ration experiments, is estimated as 7.4 $\mu l\ O_2$/mg per h. This metabolic expenditure, converted to calories per day (footnote 6, Table 3) was, on the average, about 18% of the mean daily ration for larvae given in the table. This is probably an underestimate of their metabolic requirement because the activity of larvae confined in

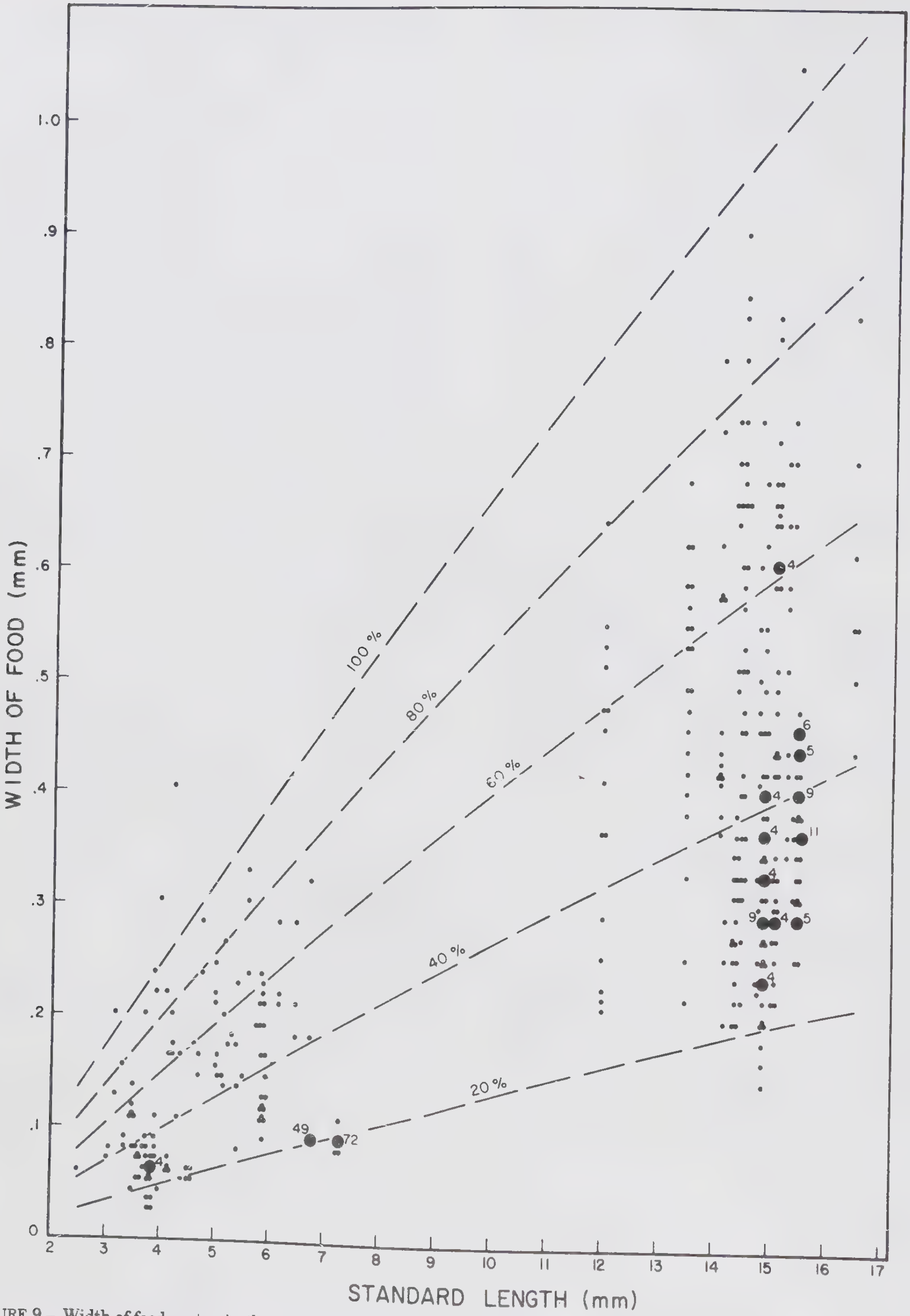

FIGURE 9.—Width of foods eaten in the sea by Pacific mackerel larvae of various standard lengths. Each small point is the width of a single prey; larger points represent multiple points for prey of the same size and number observations. Dashed lines indicate the prey width equal to 20-80% of the mouth width, or equal to the mouth width (100%), for Pacific mackerel larvae of 3-16 mm (calculated from data given in Figure 7).

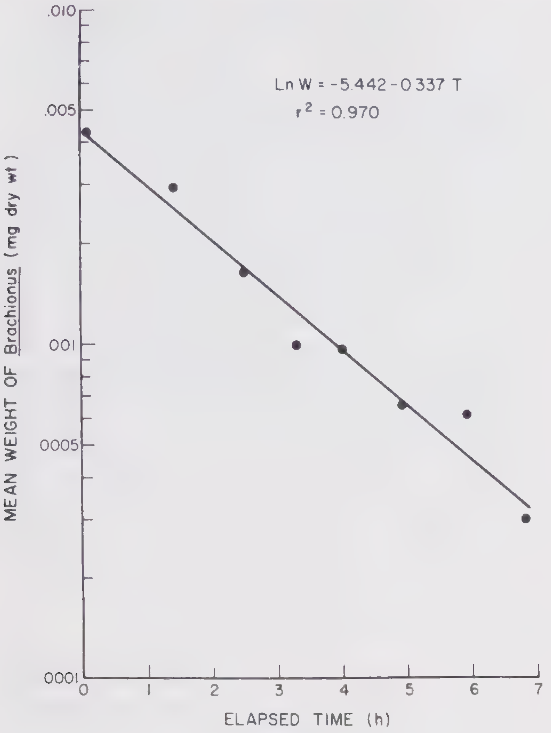

FIGURE 10.—Rate of gastric evacuation of 4.01±0.03 mm SL Pacific mackerel larvae fed *Brachionus plicatilis*. Each point represents the mean dry weight of *B. plicatilis* in guts of 13-16 larvae. Dry weight estimated by counting numbers of *B. plicatilis* in stomachs and multiplying by the mean dry weight of one *B. plicatilis* (0.16μg) (Theilacker and McMaster 1971).

Warburg flasks was probably less than that of free-swimming larvae. These respiration measurements do establish a lower limit to food ration, because the ration would have to exceed the metabolic requirement just to meet maintenance costs.

DISCUSSION

The characteristics of the embryonic period (duration of incubation and yolk-sac periods, extent of yolk reserves, size at first feeding, and ability to withstand starvation) were similar to other temperate fishes with small pelagic eggs (Lasker et al. 1970; Zweifel and Lasker 1976) and did not differ greatly from some subtropical species (Houde 1974). Small differences in these characteristics may be of importance (Houde 1974) but growth, metabolism, feeding, and swimming behavior are of more value in characterizing the early life history of Pacific mackerel.

Pacific mackerel larvae grew rapidly, completing metamorphosis (15 mm SL) in 2-3 wk. Fast growth appears to be characteristic of scombroid larvae and is even more rapid in tropical scombroids: *Auxis thazard* grew to 64 mm SL in 17 d (Harada, Murata, and Furutani 1973) and *A. tapeinosoma* grew to 49 mm SL in 18 d (Harada, Murata, and Miyashita 1973). Fast growth requires a large food ration; we found that Pacific mackerel larvae consumed about 87% of their dry

TABLE 3.—Estimate of ration, metabolism, and growth efficiency of 3-5 d old Pacific mackerel larvae fed *Brachionus plicatilis*.

Experimental conditions

			Larval weight[1]			Mean weight in stomachs[2]	
Larval age (d)	Temperature (° C)	Larval SL±2 SE (mm)	On day of ration estimation (μg)	Gain 1 d after estimation (μg)	Food density (no./ml)	No. of samples[3]	$\bar{x}$ ±2 SE (μg)
3	18.7	3.66±0.03	37.8	5.2	157	7	4.8±0.8
4	19.0	3.76±0.02	43.0	14.0	47	8	6.9±1.0
5	19.4	4.38±0.08	84.6	37.5	198	7	15.6±4.5
$\bar{x}$	19.0	3.93	55.1	18.9	134		9.1

Ration, metabolism, and growth efficiencies

	Ration[4]					
Larval age (d)	μg/d	Percent body weight/d	[5]cal/d	Metabolic rate[6] (cal/d)	Weight gain[7] (cal)	Gross growth efficiency[8] (percentage)
3	26.5	70	0.141	0.0338	0.026	20
4	38.1	89	0.203	0.0384	0.070	37
5	86.2	102	0.460	0.0756	0.188	44
$\bar{x}$	50.3	87	0.268	0.0493	0.094	33

[1] Calculated from mean larval length using relation given in Figure 4.

[2] Mean counts of *B. plicatilis* in stomach converted to weight using one *B. plicatilis* = 0.16 μg (Theilacker and McMaster 1971).

[3] Each sample consisted of 13-16 larvae; sampling began after first hour of feeding.

[4] Ration = $(r \times k \times t) + r$, where r is mean stomach contents, k is rate of gastric evacuation (0.377), and t is duration of feeding period (12 h). (From G. Stauffer, unpubl. manuscr., Southwest Fisheries Center, La Jolla, Calif.)

[5] Caloric value of *B. plicatilis* = 5,335 cal/g (Theilacker and McMaster 1971).

[6] Maintenance requirement from: 7.45 μl O_2/mg per h; 1 μl O_2 = 0.005 cal; time = 24 h; and dry weight of larvae on day ration estimated.

[7] Caloric value of weight gained assumed to equal 5,000 cal/g.

[8] Gross efficiency (dry weight) = weight gain/ration.

weight per day and weight increased from 0.034 mg to 7.5 mg over the larval period. To capture sufficient numbers of prey to support such rapid growth requires that the size of the prey and the size of the mouth increase rapidly. Our analysis of sea-caught Pacific mackerel larvae showed that the maximum size of prey did increase rapidly, more or less, in proportion to mouth size. The mean and minimum size of prey eaten by Pacific mackerel changed more slowly but the smaller prey, those less than the average size, may constitute <15% of the volume of food eaten. A similar pattern of rapidly increasing prey size with length also has been documented for *Scomber japonicus* larvae by Shirota (1970) and Yokota et al. (1961).

A dependency on larger prey and fast growth requires faster swimming to increase the volume of water searched for prey because abundance declines with increased prey size (Sheldon et al. 1972). The swimming behavior of Pacific mackerel larvae appeared consistent with this argument. Cruising speeds increased rapidly with length, roughly to the 1.8 power, and speeds of the larger larvae were at the upper end of the range, typical of larval fishes (3 SL/s) (Blaxter 1969). Higher speeds require a greater metabolic expenditure. The rate of oxygen consumption for Pacific mackerel (6-11 μl O_2/mg per h) was above that for other marine fish larvae (Blaxter 1969) indicating a higher-than-average metabolic expenditure despite the fact that the rates probably do not reflect the entire cost of high speed swimming.

Piscivorous feeding was an important behavioral trait in the early life history of Pacific mackerel because larvae were no longer limited to prey sizes equal to or less than the size of an open mouth. In piscivorous feeding, prey were seized, manipulated and the mouth greatly expanded during ingestion, permitting consumption of much larger diameter foods. In our samples of sea-caught larvae, only one stomach contained a larval fish, but the actual incidence may be higher because larvae are digested rapidly. Cannibalism, a correlate of piscivorous feeding, was common in laboratory groups after the larvae reached 8 mm SL. This also has been observed from stomach contents of the Atlantic mackerel, *S. scombrus* (Lett 1978). Cannibalism appears to be a common feature of scombroid life history; Mayo (1973) remarked that *Euthynnus alletteratus*, *Scomberomorus cavalla*, *S. regalis*, and *Auxis* sp. became cannibalistic at about 5 mm SL. He also noted that cannibalism ceased as the fish became juveniles which agrees with our observation that cannibalism ended as Pacific mackerel approached metamorphosis and began to school. The extent that cannibalism affected the form of our laboratory growth curves is unknown. Although cannibalism was high in all groups, survival was higher in groups reared at high temperatures because of the faster growth rate, which meant faster transit through cannibalistic sizes.

In summary, traits that characterize the early life history of Pacific mackerel are the interrelated characteristics of fast growth, fast swimming, high metabolism, a dependence on increasingly larger prey, and cannibalism. The high food requirements of the larvae, and the fact that in the sea they feed upon many prey substantially smaller than they are capable of eating, indicates that growth or survival in the sea might be limited by the availability of larger prey.

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EGG CANNIBALISM IN THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

Anchovies feed on their own eggs. Egg cannibalism has been reported for the Argentine anchovy, *Engraulis anchoita* (de Ciechomski 1967); Japanese anchovy, *E. japonicus* (Hayasi 1967); anchoveta, *E. ringens* (Rojas de Mendiola et al.[1]); and the northern anchovy, *E. mordax* (Loukashkin 1970). These studies give no indication whether this cannibalism was a significant part of natural mortality and incidence of cannibalism was included only as part of a general description of food habits. We provide evidence that egg cannibalism may account for a considerable proportion of natural egg mortality in the northern anchovy.

Northern anchovy feed by biting larger prey and by filtering smaller ones (Leong and O'Connell 1969). If both large and small prey are offered in the laboratory, northern anchovy in the front of the school bite the larger prey, whereas those at the end of the school feed by filtering the smaller prey (O'Connell 1972). Our laboratory observations indicate that adult northern anchovy feed on their eggs by filtering, whereas even the smallest anchovy larvae (ca. 3-4 mm long) are bitten. Such small larvae are digested beyond identification in 30 min, whereas the identifiable whole chorions and fragments may remain in northern anchovy stomachs up to 8 h although the contents of the egg (embryo and yolk) are digested after about 2 h. Northern anchovy eggs are prolate spheroids and can be easily distinguished from the spherical eggs of other pelagic spawners in the Southern California Bight.

Methods

The incidence of cannibalism in northern anchovy was estimated from an examination of 31 sets of stomach samples, usually of 10 adults each. Samples were taken at the peak of the spawning season, in the Southern California Bight, during March 1976 and 1977 (Table 1). Northern anchovy were collected in a midwater trawl or a commercial lampara net: 28 sets of collections were taken at night between sunset and sunrise and 3 sets during the day. Fish were frozen in liquid nitrogen

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[1] Rojas de Mendiola, B., N. Ochoa, R. Calienes, and O. Gomez. 1969. Contenido estomacal de anchoveta en cuarto areas de la costa Peruana. Inst. Mar. Peru Inf. Espec. (IM-27), 29 p.

TABLE 1.—Incidence of anchovy eggs in stomachs of northern anchovy collected in March 1976 and 1977 in the Los Angeles Bight.

Time of day (h)	Collection number[1]	Number fish per collection	Mean standard length (cm)	Mean weight (g)	Mean percentage full[2]	Fish with eggs (%)	Mean number eggs per fish
1300	31	25	10.0	10.2	7	68	1.9
1500	29	23	11.7	17.9	13	96	8.4
1500	30	11	12.4	19.9	14	100	6.4
2000	4	10	13.4	22.7	18	50	2.0
2000	5	10	13.4	23.3	18	10	0.1
2000	7	20	13.4	24.9	12	5	1.0
2000	17	10	10.5	11.7	17	30	.7
2100	1	11	10.7	10.0		82	2.3
2100	8	10	13.5	25.4	15	0	.0
2100	10	10	10.5	12.5		100	3.8
2100	14	10	11.6	16.2	49	40	0.6
2100	20	10	11.4	15.0	32	20	0.2
2100	23	10	12.1	19.1	38	0	.0
2200	6	10				20	0.2
2200	9	10	13.7	28.5	13	40	0.9
2200	15	10	11.4	15.9	56	50	7.1
2200	18	10	11.9	17.9	18	70	4.9
2300	11	10	11.4	16.5	14	10	0.1
2300	21	10	12.1	17.9	39	0	.0
2300	24	10	11.8	18.4	35	20	0.2
2400	2	10	10.6	12.2	4	50	3.0
2400	16	10	11.2	14.2	17	60	11.3
2400	19	10	11.5	15.3	15	90	4.6
0100	12	10	11.8	16.7	13	70	2.1
0100	13	10	11.1	14.7	25	90	22.1
0100	25	10	12.9	23.4	30	0	.0
0200	3	28	9.0	7.9	4	86	39.0
0400	27	10	12.0	17.9	31	90	20.9
0500	22	10	12.3	19.4	18	20	0.4
0500	26	10	12.3	19.3	28	30	0.9
0700	28	10	11.6	16.3	20	50	1.7
Means ± 2 SE of mean:							
Night (N = 28)			11.8±.04	17.5±1.8	23±4	42±12	4.6±3.3
Day (N = 3)			11.4±1.4	16.0±5.9	12±5	88±20	5.6±3.5

[1] Collections 1-9, night trawls, March 1976; collections 10-25, night trawls, March 1977; collections 26-28 night lampara sets, March 1977; and collections 29-31 day lampara sets, March 1976.

[2] Volume stomach contents/volume maximum contents × 100. Maximum stomach volume was size specific and derived from the relationship developed in the text.

at the time of capture, except for the day collections where formaldehyde preservation was used.

A standard oblique plankton tow (Smith and Richardson 1977) from 70 m (depth of water permitting) to the surface, was taken before and after each night trawl sample using a 1 m ring net (505 μm mesh) or Bongo net (333 μm mesh) and was preserved in 10% Formalin.[2] The 505 μm mesh net was corrected for extrusion of eggs using the coefficient of Lenarz (1972). These collections were used to estimate the abundance of northern anchovy eggs in the regions where anchovy were sampled by night trawls. For one of the day samples, two plankton tows were taken in front and two taken behind the school. The plankton samples were taken with a 0.5 m ring net with 102 μm mesh, towed for 2 min at 15 m (the depth of the school as determined acoustically). These two sets of plankton samples enabled us to measure directly the effect of feeding by a school on the egg density. No plankton tows were associated with the commercial lampara net samples.

For each fish we determined standard length (SL) and weight, numbers of eggs and larvae in the stomach, and compacted stomach volume. The stomach volume was compacted by centrifuging the contents for 6 min at 3,700 r/min and then was measured to the nearest 0.1 ml. Volumes were expressed as a percentage of the maximum stomach volume. Maximum volume (V) was determined using the same volumetric technique for northern anchovy fed to satiation with adult *Artemia salina* in the laboratory; it was expressed as a function of standard length (L) in centimeters, where $\ln V = 2.051 \ln L - 3.954$ and $r^2 = 0.759$. The length range was 4.6-13.5 cm.

To estimate the ration from observed incidence of eggs in the stomach, the rate of gastric evacuation of eggs must be known. To estimate this rate, we fed only northern anchovy eggs to 155 northern anchovy for 1 h at a density of 38 eggs/l at 15.2° C, which approximates typical spawning temperatures. After feeding, fish were transferred to a tank without food and 10-15 fish sampled at 2-h intervals until 10 h after feeding. The rate of gastric evacuation was expressed as the slope of the regression of natural logarithm of the mean eggs in the stomach as a function of elapsed time (Figure 1).

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[2] Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Incidence of Cannibalism

No relationship existed between the volume of the stomach contents and the time of collection, indicating that anchovy fed throughout the night and day (Table 1). In the night samples, the mean stomach volume was 23% of that of a full stomach and was 12% in the 3 day samples. Nearly all stomachs contained greenish to brownish material, presumably phytoplankton remains, and somewhat less frequently copepods and euphausiids were mixed with this material.

Larval fishes occurred in only 7 of the 368 stomachs (2%) and only 1 stomach contained larvae that could be identified as northern anchovy. This stomach contained 21 relatively large northern anchovy larvae; the only measurable specimen was 17 mm SL. Northern anchovy eggs occurred more frequently than larvae. Forty-two percent of the northern anchovy stomachs sampled at night contained northern anchovy eggs and 88% of those sampled in the day contained eggs. Other fish eggs were rare, occurring in 4.2±2.7 (±2 SE) of the stomachs. The mean number of anchovy eggs per stomach, including zeros, was 4.6±3.3 (±2 SE) for night samples, 5.6±3.5 for day samples, and the mean for night and day was 5.1 eggs/stomach.

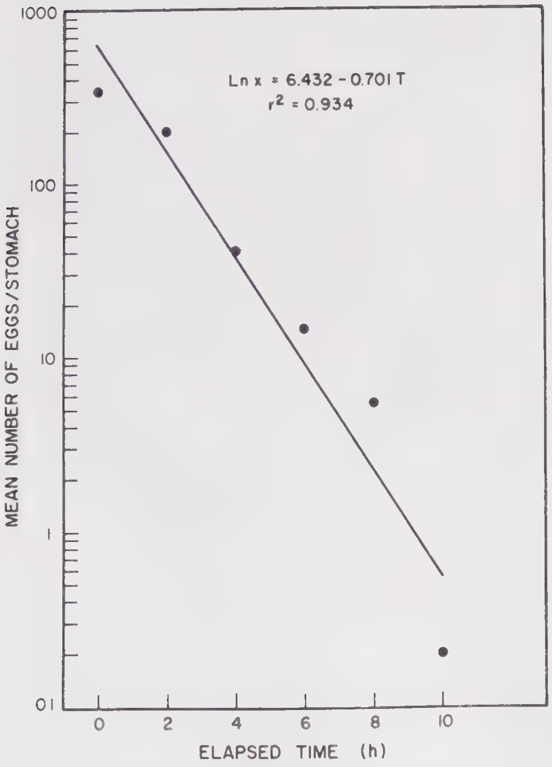

FIGURE 1.—Rate of gastric evacuation of northern anchovy fed northern anchovy eggs. Points are $\log_e$ mean number of eggs per stomach for 10-15 fish sampled at 2-h intervals after feeding.

The distribution of the number of eggs consumed per fish was highly skewed; about 90% of the eggs occurred in only 38% of the stomach samples containing eggs (19% of all stomachs). The maximum number of eggs in a single stomach was 730, which was about 32% of all the eggs found in stomachs. The patchiness of northern anchovy eggs in the sea may be responsible for this skewed distribution. The distribution was not greatly different from that of northern anchovy eggs taken in plankton samples. For example, Smith[3] found that about 90% of northern anchovy eggs occurred in only 20% of the positive plankton net hauls (N = 453).

The mean number of eggs per fish in a sample (night trawl samples) increased with egg density in the sea (Figure 2). Although variability was high (r^2 = 0.47), the 99% confidence interval about the regression coefficient was 1.107-2.095 and did not include a coefficient value of 1. This indicates that the relation was exponential and that the mean number of eggs in the stomach was not increasing in direct proportion to the mean egg abundance. Patchiness of eggs combined with selectivity in filtering could explain the exponential nature of the relationship. Certainly, oblique net tows provided only a relative measure of egg density encountered by filtering northern anchovy. Tows were begun at 70 m (below the maximum depth of northern anchovy larvae (Hunter and Sanchez 1977), or in shallow water near the bottom to insure that all eggs in the water column were sampled. Stomach contents, on the other hand, would be expected to be more closely related to the size of patches and density of eggs within egg patches and not to the integrated egg density for the water column.

Measurements of the density of eggs behind and in front of a single northern anchovy school were probably a more realistic measurement of the

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[3] P. E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1979.

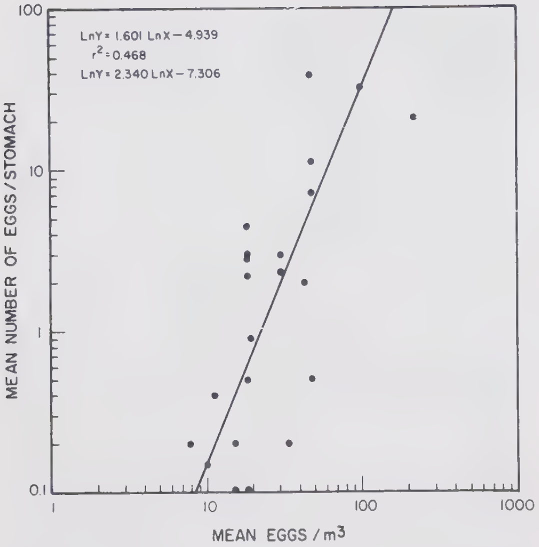

FIGURE 2.—Mean density of northern anchovy eggs in the sea and mean number of eggs in northern anchovy stomachs taken in the Los Angeles Bight in March 1976 and 1977. Points are means for 10 or more fish and means of 2-4 plankton tows. Upper equation and the line is the geometric mean regression (Ricker 1973); lower equation is the predictive equation.

actual density of eggs encountered by a school. These measurements were derived from horizontal tows made at the acoustically determined depth of the school (15 m). Estimates from the two tows taken in front of the school were 150 and 122 eggs/m^3, whereas those from the two tows taken behind the school were 75 and 54 eggs/m^3. The ratio of the means for these two sets (65:136) indicated that 48% of the eggs in the water may have been consumed by the school. Thus, a school encountering a density of about 140 eggs/m^3 may have consumed a large proportion of the eggs. The density of eggs usually encountered by schools during the peak spawning months may be in excess of 140 eggs/m^3 because the mean number of eggs per stomach for fish in this school, 1.9 ± 0.6 eggs (Collection 31, Table 1) was less than the mean for all collections, 5.1. The typical density of northern anchovy eggs within patches is not known, but a value as high as 31,000 eggs/m^3 has been recorded (Hunter in press).

The daily ration of eggs consumed by northern anchovy was estimated from the equation, $D = A \times B \times C$ where D = ration (number of eggs), B = rate of gastric evacuation (0.701), A = mean stomach contents, and C = duration of feeding (24 h). This function has been used by Tyler (1970), discussed and used by Eggers (1977), and criticized and discussed by Elliott and Persson (1978). We used for mean stomach contents (C), the mean of the averages for day and night. Using the above equation, the daily ration was 85.8 eggs/fish or 5.1 eggs/g of fish (Table 2).

The simplest method for evaluating potential effects of egg consumption is to calculate the proportion of the nightly production of eggs consumed by northern anchovy schools. Northern anchovy produce 371 eggs/g of female per spawning and during peak breeding periods, about 16% of the females spawn each night (Hunter and Goldberg 1980). Thus each night, 0.16 × 371, or 59.4 eggs are spawned per gram of female in a school. Assuming a sex ratio of 1:1, half this amount, or 29.7 eggs, are produced per gram school weight. The percentage of daily egg production consumed by a school per day (eggs consumed/eggs spawned) was 17.2% (Table 2). Smith (footnote 3) estimated the natural mortality of anchovy

TABLE 2.—Number of anchovy eggs eaten, per day, proportion of egg production consumed, and the proportion of natural egg mortality attributable to egg cannibalism in northern anchovy.

	Variable	Value	SE of mean	Data source
A	Mean eggs/stomach	5.1	[1]± 1.6	Mean of night and day averages (Table 1)
B	Rate of gastric evacuation	.701	± 0.092	See text
C	Duration of feeding (h)	24		
D	Ration, eggs/fish per day	85.80		A × B × C
E	Mean fish weight (g)	16.8	[1]± 0.9	Mean of night and day averages (Table 1)
F	Ration, eggs/grams wet weight	5.1		D/E
G	Eggs spawned/grams ovary-free female weight	389	± 30	Hunter and Goldberg 1980
H	Ratio of ovary-free weight to total female weight	.954		Hunter and Macewicz[2]
I	Eggs spawned/grams total female weight	371	± 28	G × H
J	Ratio of females spawning/night	.16	± 0.02	Hunter and Goldberg 1980
K	Ration of females/school	.50		Assumed 1:1 sex ratio
L	Eggs/gram school weight	29.7		I × J × K
M	Percent of egg production consumed/day	17.2		F/L
N	Natural egg mortality percentage/day	53		Smith and Lasker 1978
O	Percentage natural mortality from cannibalism	32.4		M/N

[1] From the night samples, Table 1.

[2] Hunter, J. R., and B. J. Macewicz 1979. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Manuscript submitted for publication.

eggs to be about 53%/d. Thus, egg cannibalism may be the cause of 32% of the natural egg mortality in northern anchovy.

Discussion

We have not tried to trace the error terms through the pyramid of calculations required to estimate the proportion of natural egg mortality attributable to cannibalism, although we give in Table 2 the standard error of the mean where estimates are available. The error in our estimate most likely will be equivalent or higher than that of the most variable parameter (i.e., mean eggs per stomach and natural mortality of northern anchovy eggs). We have no estimate of the error for the natural mortality of northern anchovy eggs but mortality rates of pelagic fish eggs are known to be high and variable; estimates range from 2 to 95% for various species (Jones and Hall 1974; Vladimirov 1975). Regardless of the uncertainties, we believe the results indicate that egg cannibalism may be a major source of egg mortality in the northern anchovy and a combination of patchiness of eggs and selectivity in filter feeding may be important in regulating the consumption of eggs.

Cannibalism is a mechanism for density-dependent regulation of fish populations (Cushing 1977), and egg cannibalism may be one of the many mechanisms regulating the size of anchovy populations. A simple model could be developed to test this hypothesis if random filtering and a random egg distribution were assumed. Although the development of such a model is beyond the scope of this paper, we wish to consider the extent our observations differ from predictions based on assumptions of randomness because this would be a critical decision in the development of the model.

The mean density of eggs in trawl associated plankton tows was 32 eggs/m^3 and the maximum filtering rate of northern anchovy of mean weight 16.8 g, is 0.158 m^3/h (Leong and O'Connell 1969). For a northern anchovy (weight 16.8 g) to obtain the estimated ration of 85.8 eggs/d, it would have to filter continuously for 17 h at a density of 32 eggs/m^3. Another approach is to estimate the percentage of the volume of the habitat that could be randomly filtered by a group of northern anchovy schools. The mean weight of northern anchovy schools in 20′ grid squares is 2.05×10^7 kg (excluding grid squares without northern anchovy) (Mais[4]); assuming the maximum depth of eggs is 30 m (Hunter and Sanchez 1977), the volume of the habitat is 2.86×10^{10} m^3. These schools would have to filter for 24 h to consume 17% of the nightly egg production. The number of hours of filtering required to obtain the average daily ration of eggs in the first calculation or to consume 17% of the egg production in the second is too high. Thus a random encounter model does not seem to account for the relatively high egg consumption that was observed and patchiness and selectivity in feeding may be the reasons.

Northern anchovy eggs exist in patches (Hewitt in press), probably in patterns similar to those described for sardine eggs (Smith 1973). Our observations of northern anchovy feeding on eggs in the laboratory indicate that filtering may be intensified when egg patches are encountered. When we added a beaker containing anchovy eggs to a 3.3 m diameter tank containing about 200 northern anchovy, they soon interrupted their circuit of the tank, formed a tight mill at the site of introduction, and filtered the region intensively. If northern anchovy display such patterns of behavior in the sea, the ration of eggs would be expected to be higher than one predicted from random filtering. Thus, present evidence indicates that an assumption of randomness would be unacceptable in a model to measure effects of cannibalism as a regulatory mechanism.

Larval cannibalism might also be significant. Northern anchovy larvae are readily eaten by adults in the laboratory. The absence of small northern anchovy larvae in stomachs may have been caused by the rapid rate of digestion (<30 min) and the low incidence of larger larvae (0.3%) caused by their low abundance in the sea. Thus, cannibalism on larvae as well as that on eggs might play a role in the regulation of northern anchovy populations but additional information is needed on feeding behavior, and on the size and density of egg and larval patches, before an evaluation of population effects can be made.

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[4] Mais, K. F. California Department of Fish and Game, Cruise Reports 76-A-3 and 77-A-3. California Department of Fish and Game, Marine Resources Region, Long Beach, Calif.

Institution of Oceanography, University of California at San Diego, La Jolla). Alec MacCall (California Department of Fish and Game, La Jolla) gave helpful suggestions regarding the interpretation of the results.

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AN ANALYSIS OF THE UNITED STATES DEMAND FOR FISH MEAL

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ABSTRACT

As fishery management plans are developed under the Fishery Conservation and Management Act of 1976, economic evaluation of management procedures will be necessary. To adequately address the economics of optimum yield, for instance, research will be required in the traditional economic subjects of demand, production and costs, industrial organization, and international trade. This paper addresses the domestic demand for the primary industrial fishery product—fish meal. In developing the demand model the important points are: 1) choice of empirical variables for inclusion in the model, 2) determination of appropriate functional form of the demand equation, 3) treatment of the "simultaneity bias" problem, and 4) choice between a static (or equilibrium) model and a dynamic model. The paper presents maximum likelihood estimates of both the static and dynamic models. With either model the price elasticity of demand is high when fish meal price is low, and is low when price is high.

Analysis of prices and market demand relationships for fish is of increased importance since the enactment of the U.S. Fishery Conservation and Management Act of 1976 (FCMA[2]). The new law not only establishes a zone of Federal control over fisheries from 3 to 200 mi offshore, but it also establishes national standards for fishery management plans which include economic and social aspects. A key concept is that of "optimum yield"—that rate of annual catch "which will provide the greatest overall benefit to the Nation" (FCMA, Sec. 3(18)). Economic benefits to the nation accrue primarily through the consumption of fishery products which are sold in more-or-less free and competitive markets. Market prices can be expected to vary in response to changes in the annual yields permitted under fishery management plans. These price impacts, along with associated changes in real income, cannot be neglected in the development of appropriate management methods. The demand analysis presented in this paper will assist in the determination of optimum yield for fisheries which contribute to the U.S. fish meal supply.

Fish meal is a primary product of the Atlantic and Gulf of Mexico menhaden fisheries and the California anchovy fishery. It also appears as a byproduct of groundfish and tuna processing. It is used as a high protein supplement most commonly mixed with corn, soybean, or cottonseed meal; meat byproduct meal; and vitamins and minerals for feeding to broilers, layers, and turkeys. According to J. Vondruska,[3] fish meal is also used in feeds for mink and other fur-bearing animals, farmed fish, laboratory animals, livestock, and household pets. About 80% of fish meal consumed in the United States goes into poultry feed. A high level of metabolizable energy and such nutritional elements as riboflavin, pantothenic acid, niacin, choline, and several amino acids are contributed to animal feed by the addition of fish meal (Karrick 1963). Most of these constituents are available in high protein vegetable meals, but fish has a particularly high concentration of the amino acids lysine and methionine.

Because the lysine and methionine are necessary for fast growth in chicks, feed mixers generally seek to include between 2 and 8% fish meal in broiler rations. With >8% fish meal, the poultry tends to pick up a "fishy" flavor. With <2% fish meal, further substitution of vegetable protein meals for fish meal will result in slower growth because the fixed quantity of feed eaten per day per chick cannot contain the ideal mix of amino acids. When fish meal is extremely high priced or

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[2] Public Law 94-265, 94th Congress, 2d Session 13 April 1976, 16 USC 1801 et seq. (Suppl. 1977). Hereafter, FCMA.

[3] J. Vondruska. 1979. Postwar production, consumption, and prices of fish meal. Unpubl. manuscr., 66 p. National Marine Fisheries Service, 3300 Whitehaven St., N.W., Washington, DC 20235.

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unavailable, the lysine and methionine content of the feed can be augmented with synthetic proteins. Kolhonen (1974) described the development of synthetic methionine and lysine for use in feed formulas.

Linear programming has been widely adopted by formula feed manufacturers in the United States and western Europe (Kolhonen 1974). Least-cost combinations of feed constituents needed for adequate nutrition are quickly and accurately computed for any vector of constituent prices. Thus, the demand for feed ingredients is expected to exhibit great sensitivity to relative prices. In a recent examination of demand for agricultural feed ingredients, Meilke (1974) reported that price elasticities are generally >2 in absolute value. It is expected that the demand for fish meal will be elastic also, at least when available quantities allow the feed formula manufacturers to include between 2 and 8% fish meal in poultry rations. When the supply of fish meal is low enough to jeopardize the maintenance of at least 2% fish meal, the demand may become inelastic. Thus, one hypothesis to be tested is that the own price elasticity of demand for fish meal falls with increasing price and decreasing quantity.

Markets for fish meal in the United States are, for obvious reasons, concentrated in the poultry-producing regions—California, Arkansas, and states in the Deep South. Domestic production of fish meal occurs mainly in California, the Gulf Coast States, and the South Atlantic States. In some years, however, much of the domestic supply is imported from major foreign producers such as Peru. Foreign meal is a perfect substitute for the domestic product, but the supply of foreign meal has undergone tremendous fluctuations due to variations in fish stocks (especially the Peruvian anchoveta, *Engraulis ringens*). Domestic supplies have also been strongly influenced by uncontrolled variations in domestic stocks (especially menhaden *Brevoortia tyannus* and *B. patronus*) and by administrative decisions of fishery management agencies (California's anchovy, *Engraulis mordax*, fishery, e.g., see Pacific Fishery Management Council 1978: 31660-31664). On the supply side of the domestic market, therefore, the major fluctuations are not price induced, but are due to exogeneous factors. On the demand side the poultry industry experienced a steady expansion starting in the early 1950's and continuing until about 1970.

DEVELOPMENT OF DEMAND MODEL

Demand and price analysis has been a cornerstone of applied economic research since the 1930's (Working 1927; Schultz 1938; Wold and Juréen 1953). Agricultural economists have been particularly active in developing demand models for commodities. Research on demand for fish is of more recent vintage but differs in few important respects from that for agricultural commodities. For an excellent review of the historical development of demand analysis, see Waugh and Norton (1969). Among the methodological issues addressed in applied demand studies are: 1) specification of the demand model, 2) development of appropriate functional forms, 3) treatment of simultaneity bias in market demand and supply function estimates, and 4) incorporation of dynamic response mechanisms in the demand model. These issues are discussed seriatim.

Specification

The specification of a demand model consists of the choice of dependent and independent variables. Annual quantity demanded, as measured by quantity purchased, should be the dependent variable. Purchased quantities are difficult to obtain, however, while production, import, and export statistics are well documented. Also, meals derived from different sources differ in protein content and sell at different prices. Both the quantities and the prices must be aggregated such that they represent a reasonably homogeneous commodity. Fish meal quantities (Table 1, columns 1-6) are converted to a protein equivalent basis by multiplying the quantity of each type of meal by the prevailing percentage of protein content. The total available domestic quantity, computed by summation of protein equivalent fish meals and subtraction of exports, is listed in Table 1, column 7. Similarly, since the prices of the various fish meal types (Table 2, columns 1-4) are based on protein content, each price is converted to a protein basis. The aggregate price of fish meal introduced as an independent variable in the demand model is the average price per unit protein for all meal supplied to the U.S. market (Table 2, column 5). Some specification error may enter the model because domestic supply rather than quantity purchased is used for the dependent variable, but this problem is unavoidable with available information.

TABLE 1.—United States fish meal supplies, 1955-76 (thousands of metric tons). (National Marine Fisheries Service 1975, 1977.)

Year	(1) Menhaden	(2) Tuna	(3) Anchovy	(4) Other[1]	(5) Imports	(6) Exports	(7) Total supply protein basis[2]
1955	172.9	21.2	0.0	37.6	88.9	n.a.[3]	195.8
1956	191.1	23.9	0.0	44.1	82.0	n.a.	207.5
1957	156.4	23.3	0.0	51.3	73.7	n.a.	185.3
1958	143.4	23.0	0.0	50.2	91.1	n.a.	188.0
1959	203.1	23.0	0.0	43.1	120.6	n.a.	238.8
1960	198.1	24.0	0.0	33.1	119.4	n.a.	229.6
1961	224.6	19.2	0.0	28.8	197.6	n.a.	291.0
1962	217.5	24.1	0.0	31.5	228.9	n.a.	311.4
1963	167.1	24.5	0.0	33.4	341.4	n.a.	355.7
1964	145.4	19.1	0.0	39.6	398.3	n.a.	380.4
1965	159.7	23.0	0.0	37 3	245.5	n.a.	290.4
1966	122.5	23.0	4.1	42.9	406.2	n.a.	378.6
1967	108.1	23.1	5.1	46.5	591.0	n.a.	492.9
1968	129.9	26.1	2.5	47.4	775.9	n.a.	626.7
1969	144.7	24.4	10.3	42.1	325.1	n.a.	343.6
1970	171.1	24.2	14.7	23.2	227.8	4.3	284.9
1971	200.4	26.6	6.9	22.7	256.9	9.2	314.4
1972	175.6	39.2	10.1	23.8	355.6	9.5	373.2
1973	171.3	39.6	20.0	22.4	62.1	33.3	171.4
1974	185.0	43.7	12.8	23.0	62.0	50.3	167.2
1975	173.6	33.7	25.1	20.9	107.4	10.7	215.0
1976	192.9	36.4	19.9	22.0	127.4	30.0	226.7

[1] Primarily from offal, waste, and scrap from groundfish and herring.

[2] Converted to protein as follows: menhaden, exports, and other meal assumed to be 60% protein; anchovy and imports assumed to be 65% protein; tuna meal assumed to be 55% protein. Total supply is production plus imports minus exports.

[3] n.a. means data not available.

TABLE 2.—Annual average prices for various fish meals and average price per unit of protein in fish meal in the United States. (National Marine Fisheries Service 1975.)

Year	(1) Menhaden	(2) Tuna	(3) Domestic anchovy	(4) Peruvian anchovy	(5) Average price per unit protein in fish meal	
					Actual[1]	Deflated[2]
	-------*dollars per metric ton of meal*-------					
1955	123.4	130.7	—	—	1.99	4.34
1956	121.7	121.7	—	—	1.97	4.16
1957	117.7	114.8	—	121.5	1.95	4.01
1958	125.0	124.8	—	128.2	2.01	4.19
1959	116.2	117.1	—	131.9	1.95	3.94
1960	84.4	86.0	—	86.1	1.39	2.80
1961	106.4	99.7	—	100.0	1.69	3.40
1962	112.6	109.5	—	111.2	1.81	3.64
1963	114.1	106.2	—	109.7	1.76	3.58
1964	119.3	115.8	—	119.7	1.88	3.81
1965	152.9	143.2	—	140.3	2.30	4.63
1966	146.1	134.4	137.3	141.9	2.23	4.33
1967	123.8	117.6	117.5	118.1	1.86	3.57
1968	131.8	114.2	110.7	118.8	1.88	3.53
1969	158.1	132.6	137.9	142.5	2.31	4.24
1970	167.4	155.4	156.0	176.4	2.72	4.72
1971	143.3	128.0	140.4	150.7	2.33	3.92
1972	168.3	141.4	154.1	162.6	2.59	4.15
1973	433.8	359.6	365.5	409.8	6.75	9.70
1974	250.5	245.5	270.3	260.6	4.15	4.99
1975	216.9	206.3	214.8	226.5	3.54	3.88
1976	314.3	347.8	247.5	309.9	4.92	5.15

[1] For each meal, price per unit protein equals price per ton divided by percent protein. Average price computed by weighting the price per unit protein for each meal by the proportion of U.S. fish meal protein supplied by that meal.

[2] Deflated by Wholesale Price Index, all commodities (January 1977 = 100).

In addition to the price of fish meal, the demand model should contain independent variables representing 1) the prices of close substitute products, 2) prices of complementary products, and 3) the level of production activity that governs the demand for fish meal. Several high protein meals (e.g., soybean, cottonseed, meat, and bone meals) are potential substitutes for fish meal in poultry rations. Soybean meal is the most common substitute, and its price is used as an independent variable in the demand model. The price of corn meal (Table 3, column 2) is introduced as a complementary product price. Demand for fish meal is expected to increase when the price of a substitute product increases, and is expected to decrease when the price of a complementary product increases. Finally, the overall production of poultry products would cause shifts in the level of demand for fish meal independently of the prices. The poultry and egg production index (Table 3, column 3) is adopted as the appropriate measure of this factor.

In summary, the fish meal demand model is specified as follows:

1) Quantity demanded, the independent variable, is represented by annual production plus net imports of protein-equivalent meal.
2) Annual price of fish meal is measured as the weighted average of the prices per unit protein for all domestically supplied meals.

TABLE 3.—Exogenous variables in the fish meal demand model.

Year	Price of domestic soybean meal[1]	Price of domestic corn[2]	Poultry and egg production index[3] (1976 = 100)
	-------*dollars per metric ton*------		
1955	51.6	2.24	58
1956	46.5	2.30	63
1957	42.7	2.06	64
1958	50.8	1.99	68
1959	51.3	1.94	70
1960	48.2	1.84	70
1961	57.3	1.80	75
1962	60.3	1 80	75
1963	65.8	2.00	77
1964	62.8	1.99	80
1965	64.9	2.07	83
1966	76.0	2.18	88
1967	69.4	2.06	92
1968	70.3	1.80	90
1969	67.6	1.96	92
1970	71.8	2.19	97
1971	70.7	2.15	98
1972	95.2	2.10	100
1973	216.3	3.57	97
1974	127.8	5.20	97
1975	112.6	4.71	94
1976	147.5	4.37	100

[1] Forty-four percent protein. Simple average price at Decatur, Ill., from National Marine Fisheries Service (1977).

[2] Price of No. 2 yellow corn, Chicago. USDA, ERS, Poultry and Egg Situation, PES-294, 1965-77.

[3] From Schultze et al. (1979).

3) Annual domestic price of corn and annual domestic price of soybean meal are introduced as complementary and substitute product prices.
4) The trend in aggregate demand over time is accounted for by the aggregate poultry and egg production in the United States.

All of the variables expressed in dollars are deflated by the Wholesale Price Index to eliminate spurious correlations caused by the inflationary trend.

Functional Form

Demand studies typically utilize least squares regression methodology with either a linear or a log-linear equation. As noted by Chang (1977), however, there is no a priori reason to choose one of these forms. Each form imposes some fairly strict conditions upon the characteristics of the demand function which may contradict theoretical considerations or actual experience. Linear equations imply that the elasticity of demand with respect to any independent variable is a decreasing function of that variable; a log-linear equation implies constant elasticities. Chang suggests that the income elasticity of demand for meat should fall with rising income. A similar consideration applies to fish meal demand. At low prices, feed manufacturers would use near maximum amounts of fish meal allowable and could easily substitute soybean meal for fish meal. With relatively high fish meal prices, feed manufacturers would use a smaller proportion of fish meal, but as price rises further it would be increasingly difficult to maintain desired quantities of lysine and methionine by substitution of soybean meal. Thus it is clearly unwarranted to rule out increasing price elasticity through a priori choice of functional form.

The function to be fitted by regression analysis can be chosen by determining the appropriate transformation of variables for the linear least squares procedure. The log-linear transformation is a special case of a parametric family of transformations introduced by Box and Cox (1964). The parameter defines the transformation

$$x^* = (x^\lambda - 1)/\lambda. \tag{1}$$

Equation (1) is linear for $\lambda = 1$, and becomes logarithmic as λ approaches zero. The demand function is expressed as

$$q^* = b_0 + b_1 x_1^* + \ldots + b_k x_k^* + u \tag{2}$$

where q is the quantity demanded, the x's are the independent variables affecting demand, u_t is a stochastic error term, and the b_i and λ are parameters to be determined. The superscript * indicates that the variable has been transformed as in Equation (1).

Price elasticity of demand is defined as the absolute value of the ratio of percentage change in quantity demanded to percentage change in price. Assuming that the first independent variable is the price, $E = \left|\frac{\partial q}{\partial x}\right| \cdot \left(\frac{x_1}{q}\right)$. From Equation (2) we get

$$E = |b_1| (q/x_1)^{-\lambda}. \tag{3}$$

The elasticity defined in Equation (3) is an increasing function of x_1 when $\lambda>0$, and is a decreasing function of x_1 when $\lambda<0$. Thus the estimate of the transformation parameter λ provides a test of whether the price elasticity increases, decreases, or remains fixed along the demand curve.

Simultaneity Bias

In economic theory, the supply and demand curves interact to determine the market price. Over a period of time, shifts in both supply and demand factors cause the market price and observed quantities of products to vary. Without these shifts, only one price and quantity would be observed, making it impossible to estimate a demand or supply curve. When the demand curve remains stable, the observed price-quantity pairs "trace out" the demand curve with, of course, some stochastic error, and a regression analysis will result in a demand curve estimate. When the supply curve remains stable, the observed data will fall along the supply curve, and a regression analysis of the price-quantity relationship results in a supply curve estimate. If shifts in both demand and supply occur, the resulting data will not unambiguously identify either of these two curves, and an ordinary least squares regression will generally result in a set of parameters reflecting neither the supply curve nor the demand curve. In this case the estimated parameters are said to suffer from simultaneity bias.

The general statistical problems associated with estimation of individual structural relationships in a simultaneous equation system were first examined by Haavelmo (1943). Development of appropriate statistical methods for estimating simultaneous equation systems has been a major area of research for econometricians over the last two decades (Kmenta 1971). In estimating the demand curve for fish meal, however, direct regression estimates seem appropriate, because most of the observed variations in annual fish meal supplies are due to exogeneous shifts rather than price-induced movements along a stable supply curve. Production of fish meal is subject to wide fluctuations due to uncontrolled variations in the fish stocks exploited (Kolhonen 1974). At the same time, formula feed and poultry industries have remained relatively stable during the last 20 yr except for the secular growth accounted for in the analysis. Under conditions in which the random shifts in supply are much greater than the corresponding shifts in demand, the ordinary least squares procedure results in no significant simultaneity bias (Rao and Miller 1971).

Lagged Response Mechanisms

The use of annual price and quantity data for estimating the demand function requires that the response to a change in price occurs rather rapidly, at least within a period of time much shorter than a year. Since most domestic formula feed manufacturers employ professional nutritionists and cost-minimizing computer routines in calculating formulas, the response to changes in the vector of prices is probably rapid. If so, each annual quantity consumed may be assumed to represent at least approximately an equilibrium demand response to the set of independent variables. The assumption of rapid response and equilibrium approximation, however, has not been directly verified. In the interests of rigor it is useful, therefore, to consider alternative assumptions.

A lagged response to a change in price may occur due to rigidities in mixing procedures or personnel, inventory management problems, or time lags in renegotiating contracts for supply of input or sales of products. If any of these factors results in a sluggish response in the substitution between fish meal and other protein meals, the effect of a price change may be drawn out over several periods of time. A fairly simple model for representing a lagged response is the "partial adjustment model" originally developed by Nerlove (1958). Corresponding to any given level of the independent variable, p, there is an optimal or desired level of the dependent variable q. For a demand function with one independent variable, the level of demand fully adjusted to input prices by formula manufacturers represents the desired level of fish meal usage:

$$q_t^d = b\,p_t + u_t \tag{4}$$

where the superscript d signifies desired level.

Because purchasers of meal cannot immediately adjust to this desired level of usage, the demand Equation (4) is not directly observable. By assuming a simple structure to the adjustment process, however, an estimable equation is obtained. The partial model assumes that a fixed percentage of the adjustment to desired level is made each year. This introduces the difference equation

$$q_t - q_{t-1} = \gamma(q_t^d - q_{t-1}). \tag{5}$$

Solving this for q_t and substituting from Equation (4) yields

$$q_t = b\,\gamma\,p_t + (1-\gamma)q_{t-1} + \gamma u_t. \tag{6}$$

The adjustment parameter, γ, must be a positive number ≤ 1. Larger values of γ imply more rapid adjustment to changes in the independent variable. The impact of a unit change in p_t is distributed over time in an exponentially decaying fashion with successive annual changes in q being equal to $b\gamma$, $b\gamma(1-\gamma)$, $b\gamma(1-\gamma)^2$, and so forth. The ultimate change in q due to a change in p is

$$\Delta q = b\Delta p \sum_{j=0}^{\infty} \gamma(1-\gamma)^j = b\Delta p \tag{7}$$

where j = lag. The elements in the sequence under the summation sign are all positive fractions, and sum to one, so that the sequence can be treated like a probability distribution. Each element represents the percentage of the total effect occuring in year t, and the mean of the distribution, $(1-\gamma)/\gamma$, represents the mean lag in the adjustment process. Distributed lag models like that in Equation (4) result from other conceptual models such as models of expectations formation or habit formation. And the exponentially distributed lag is but one of a large class of more complex lag models (Griliches 1967; Kmenta 1971; Rao and Miller 1971).

Application of the partial adjustment model to the demand Equation (2) results in the following:

$$q^*_t = a_0 + \sum_{i=1}^{4} a_i x^*_i + a_5 q^*_{t-1} + u_t \qquad (8)$$

where the coefficients a_i can be interpreted in terms of the coefficients of Equation (2) as follows:

$$a_0 = \gamma b_0$$
$$a_i = \gamma b_i;\ i = 1, \ldots 4$$
$$a_5 = (1 - \gamma).$$

STATISTICAL PROCEDURES

For a given value of the transformation parameter, λ, the coefficients of either the equilibrium model [Equation (2)] or the partial Adjustment model [Equation (8)] can be estimated by the ordinary least squares method. Two statistical issues requiring further development, however, are the selection of the "best" value for λ, and the test for significance of the lagged adjustment parameter. An appropriate procedure for estimation of λ was first suggested by Box and Cox (1964). The procedure is more clearly explained in the linear regression context by Kmenta (1971) and is reviewed by Chang (1977). For a fixed value of λ, the linear regression procedure yields an estimate of the error variance $\hat{\sigma}^2$. Box and Cox showed that the maximized log likelihood is, except for a constant,

$$L_{\max}(\lambda) = -(N/2) \log \hat{\sigma}^2(\lambda) + (\lambda - 1)\Sigma \log q_i. \qquad (9)$$

A maximum likelihood estimate of λ can, therefore, be found by searching through successive values of λ to maximize Equation (9). The use of this likelihood function implies, of course, that the error terms conform to full normal theory assumptions, i.e., that the u_t are independently normally distributed with zero mean and constant variance. An approximate 100% $(1 - \alpha)$ confidence region for λ is defined by

$$L_{\max}(\hat{\lambda}) - L_{\max}(\lambda) < \tfrac{1}{2}\, \chi_1^2(\alpha) \qquad (10)$$

where $\chi_1^2(\alpha)$ represents the value of the chi-square distribution with 1 df (Box and Cox 1964).

Serial correlation in the errors of the regression model raises problems in the interpretation of the test statistics for the nonlagged variables and the lagged adjustment parameter, and contradicts the assumptions of the log likelihood function. Careful examination of the hypotheses and statistics regarding the residuals of the regression equation is clearly necessary. Existence of serial correlation in the errors of the static demand model can be tested with the Durbin-Watson statistic. If no serial correlation is apparent in the residuals, then neither the distributed lag model nor the serial correlation model need be considered. If serial correlation is present in the residuals of the static model, then the problem is to distinguish between the distributed lag model and the serial correlation model.

Griliches (1967) showed that the serial correlation and lagged adjustment models cannot be distinguished by a simple t-test on the adjustment parameter. For example, if errors generated by a first order Markov process, i.e., $e_t = se_{t-1} + u_t$, occur in a regression equation, the coefficients of the lagged variables may be judged significant by the usual t-test even though there is no real lagged response in the underlying structural relationship. Similarly, it can be shown that serially correlated residuals will occur if a nonlagged model is mistakenly fit to data from an inherently dynamic process.

Although there is no fully satisfactory method for determining which model is the truth, Griliches (1967) developed a provisional test. Briefly, the serial correlation model is

$$q_t = a_0 + \sum_i a_i x_{it} + e_t \qquad (11a)$$

$$e_t = se_{t-1} + u_t \qquad (11b)$$

where s is a positive fraction and u_t is a nonserially correlated error term. From Equation (11a), $e_{t-1} = q_{t-1} - a_0 - \Sigma_i a_i x_{it-1}$; so that $e_t = s(q_{t-1} - a_0 - \Sigma_i a_i x_{it-1}) + u_t$. Substituting this into Equation (11a) yields

$$q_t = (1 - s)a_0 + \sum_i (a_i x_{it} - b_i x_{it-1}) + s\, q_{t-1} + u_t. \qquad (12)$$

When Equation (12) is computed, the serial correlation model implies that $a_i s = -b_i$ for each i. Griliches suggested that the first-order serial correlation model be rejected if these four equalities do not appear to hold. Thus, there are four hypotheses of the following form:

$$H_0: (b_i + sa_i) = 0. \tag{13}$$

An approximate sample variance for $(b_i + sa_i)$ is computed by the "delta method" described by Seber (1973). The expression for approximate variance of a function of a vector of random variables, $G(x)$, is

$$\mathrm{v}[G(x)] = \Sigma v(x_i)\left(\frac{\partial G}{\partial x_i}\right)^2 + 2\sum_{i<j}\Sigma \operatorname{cov}(x_i\, x_j)\left(\frac{\partial G}{\partial x_i}\right)\left(\frac{\partial G}{\partial x_j}\right). \tag{14}$$

Assuming that the estimate of $(b_i + sa_i)$ from the regression equation is approximately normally distributed, the following ratio will be approximately distributed as an F-statistic with 1 and $(n - r)$ df (where r is the number of regression parameters estimated):

$$(b_i + sa_i)^2/\mathrm{v}[b_i + sa_i] \approx F(1, n - r). \tag{15}$$

Since the serial correlation model requires each of the four hypotheses to hold, a definite rejection of one or more of the hypotheses may be taken as evidence against the serial correlation model and in support of the partial adjustment model. Because of the lack of rigor in the suggested testing procedure, however, caution must be exercised in drawing conclusions.

RESULTS

Ordinary least squares estimates of the static demand Equation (2) were computed for a range of values for the transformation parameter λ. The regression coefficients and statistics of most interest are listed in Table 4. A value of $\lambda = -0.55$ maximizes the log likelihood function, but the 95% confidence interval for λ is 0.2 to -1.4. The interval includes the logarithmic transformation ($\lambda = 0$), but not the linear transformation ($\lambda = 1$). The negative value of λ, which implies a price elasticity of demand that decreases as quantity decreases, conforms to expectations. The signs of all the coefficients are also consistent with prior expectations; demand is diminished by increasing price of fish meal or corn meal, and is increased by increasing price of soybean meal and by expanding poultry and egg production. Application of t-tests to the coefficients of the equation with $\lambda = -0.55$ indicates statistical significance with 99% confidence for the coefficients of fish meal price and corn meal price, and with 90% confidence for the coefficient of soybean meal price. The poultry and egg production index appears to be an insignificant influence on fish meal demand by the t-test. But this is insufficient reason for eliminating a theoretically important variable from the equation.

The squared multiple correlation coefficient, $r^2 = 0.73$, indicates a reasonably "good fit" for a demand equation estimate from time-series data.

TABLE 4.—Regressions for determining maximum log-likelihood of static demand function. P_f = price of fish meal, P_s = price of soybean meal, P_c = price of corn feed, Q_p = poultry and egg production index. Superscript * indicates Box-Cox transformation expressed in Equation (1).

Transformation parameter (λ)	Intercept	Coefficient				R^2	D-W[1]	Lmax(λ)
		P_f^*	P_s^*	P_c	Q_p^*			
0.5	44.184	−10.144	9.588	−8.597	0.816	0.695	0.754	−91.21
[2]0.2	12.499	−2.620	2.174	−2.532	0.545	0.714	0.716	−89.70
0.0	6.054	−1.064	0.812	−1.125	0.413	0.722	0.704	−88.97
−0.20	3.324	−0.432	0.305	−0.501	0.311	0.727	0.705	−88.48
−0.50	1.731	−0.112	0.071	−0.150	0.199	0.730	0.725	−88.14
[3]−0.55	1.592	−0.089	0.056	−0.123	0.184	0.730	0.731	−88.13
	(5.108)	(−2.602)	(1.864)	(−3.489)	(0.976)			
−0.60	1.474	−0.071	0.044	−0.100	0.171	0.730	0.735	−88.14
−0.70	1.282	−0.455	0.027	−0.067	0.146	0.729	0.751	−88.18
−1.0	0.929	−0.012	0.007	−0.020	0.088	0.724	0.801	−88.56
−1.2	0.789	−0.005	0.003	−0.009	0.061	0.719	0.839	−89.02
[2]−1.4	0.687	−0.002	0.001	−0.004	0.042	0.711	0.879	−89.61

[1] D-W stands for Durbin-Watson statistic.

[2] Indicates approximate 90% confidence interval for λ.

[3] Indicates maximum likelihood estimate (t-values in parenthesis).

The Durbin-Watson statistic (0.731) is below the lower critical value (d_l = 0.86 for 21 observations and 4 parameter estimates), indicating significant serial correlation in the errors of the demand model. As suggested above, this serial correlation may be caused by incorrect specification of a static model when a dynamic adjustment model would be more appropriate, or it may reflect true serial correlation in the errors which may in turn be due to some other source of misspecification.

Following the suggestion by Griliches (1967), a regression equation with lagged dependent and independent variables was computed (Table 5). The F-statistics for the four hypotheses associated with the serial correlation model range from 0.119 to 6.516. The critical value for each hypothesis (with $P<0.05$ and for 1 and 11 df) is 4.84. Clearly, only one of the four hypotheses, the one associated with the soybean price, can be rejected with great confidence. Even this may be misleading, because the probability of wrongly rejecting at least one of four hypotheses at the 5% level is 0.183[4]. Due to the provisional nature of the test procedure and the inconclusiveness of the result, it is useful to consider both the static and distributed lag models as plausible representations.

The distributed lag model [Equation (8)] was estimated by ordinary least squares for several values of the transformation parameter λ. Regression coefficients and pertinent statistics for the distributed lag model are listed in Table 6. The log-likelihood function is greatest for λ = −0.3, and the approximate 95% confidence interval for λ is −1.0 to 0.22. As in the earlier nonlagged model, the coefficients of the independent variables have the appropriate signs. Since the coefficient of the lagged dependent variable can be interpreted via Equation (5) as one minus the rate of adjustment parameter, the partial adjustment parameter is 0.503. This implies an average lag of slightly less than one. As expected, buyers of fish meal generally adjust to changing conditions and prices within a year.

TABLE 5.—Estimates for demand function parameters with all variables lagged.[1] Transformation parameter, λ, equals −0.55; and all symbols are as explained in Table 4. R^2 = 0.855.

Variable	Estimated coefficient	SE	F-statistic[2]
$P_f^*(t)$	−0.07521	0.03208	0.455
$P_f^*(t-1)$	0.01861	0.03258	
$P_s^*(t)$	0.07498	0.0297	6.516
$P_s^*(t-1)$	0.03765	0.03609	
$P_c^*(t)$	−0.2059	0.07897	0.119
$P_c^*(t-1)$	0.1159	0.04239	
$Q_p^*(t)$	1.3352	0.5497	4.006
$Q_p^*(t-1)$	−1.5422	0.5309	
$q^*(t-1)$	0.5164	0.1979	—

[1] $q^*(t) = a_0 + a_1P_f^*(t) + b_1P_f^*(t-1) + a_2P_s^*(t) + b_2P_s^*(t-1) + a_3P_c^*(t) + b_3P_c^*(t-1) + a_4Q_p^*(t) + b_4Q_p^*(t-1) + a_5q^*(t-1)$

[2] The hypothesis to be tested is $(b_i + a_i a_S) = 0$; and the corresponding F-statistic is $F_i = (b_i + a_i a_S)^2 / \mathrm{Var}(b_i + a_i a_S)$

DISCUSSION

Both the static demand model and the partial adjustment model provide reasonable levels of statistical fit to the historical data series and the signs and magnitudes of the regression

TABLE 6.—Regression equations for determining maximum log-likelihood of distributed lag form of demand function. P_f = price of fish meal, P_s = price of soybean meal, P_c = price of corn feed, Q_p = poultry and egg production index, q_{t-1} = quantity of fish meal, lagged. Superscript * indicates Box-Cox transformation expressed in Equation (1).

Transformation parameter (λ)	Intercept	Coefficient P_f^*	P_s^*	P_c^*	Q_p^*	q_{t-1}^*	R^2	$L_{\max}(\lambda)$
1.0	297.904	−103.141	105.367	−21.018	0.694	0.468	0.766	−81.133
0.6	40.639	−16.897	13.097	−3.821	0.537	0.485	0.800	−83.953
0.1	4.122	−1.792	0.902	−0.482	0.389	0.498	0.822	−81.507
0	2.761	−1.147	0.522	−0.323	0.363	0.499	0.824	−81.259
−0.2	1.373	−0.470	0.170	−0.147	0.314	0.498	0.825	−81.014
[1]−0.3	1.030	−0.301	0.098	−0.100	0.291	0.497	0.824	−81.013
	(1.396)	(−3.567)	(1.161)	(−0.840)	(1.189)	(2.907)		
−0.4	0.809	−0.193	0.056	−0.068	0.268	0.494	0.822	−81.090
−0.5	0.665	−0.124	0.031	−0.047	0.247	0.491	0.819	−81.239
−1.0	0.404	−0.013	0.002	−0.008	0.153	0.458	0.795	−82.853

[1] Indicates maximum likelihood estimate (t-values in parentheses).

---

[4] The probability of type 1 error in a single test is 0.05. If four tests are made the probability of making at least one type 1 error is one minus the probability of making no type 1 errors, i.e., 1 − $(0.95)^4$.

coefficients satisfy prior expectations. Because it yields a significantly higher r^2, and because the test for serial correlation suggested by Griliches (1967) lends it support, I tend to favor the distributed lag model. But the evidence is not really conclusive. For one thing, the "Griliches test" looks only for first-order serial correlation, and it will probably fail to give correct guidance when more complex residual generating processes are present. Another difficulty is the lower precision of the regression coefficients in the distributed lag model. The importance of this depends upon how the demand function is to be used. In fisheries management applications the most important use of the demand model will be for predicting price effects resulting from changes in annual production.

To compare the two demand models, the equations are transformed to give quantity demanded in natural units (tons of fish meal proteins) and the 1976 values of independent variables other than fish meal price are inserted. The resulting relationships between price and quantity are

$$q_t = \left[-0.00389 + 0.04916\left(\frac{P_f^{-0.55} - 1}{-0.55}\right)\right]^{\frac{1}{-0.55}} \qquad (16)$$

for the static demand model, and

$$q_t = \left[-0.03486 + 0.18001\left(\frac{P_f^{-0.3} - 1}{-0.3}\right)\right]^{\frac{1}{-0.3}} \qquad (17)$$

TABLE 7.—Demand predictions ($\hat{q}$) and price elasticities (E) for static demand ($\lambda = -0.55$) and partial adjustment ($\lambda = -0.3$) models.

Price of fish meal protein (P_f)	Static demand model		Partial adjustment model	
	$\hat{q}$	E	$\hat{q}$	E
2	852.5	2.49	4,971.0	6.26
4	295.2	0.95	372.3	2.34
6	215.1	0.64	168.8	1.63
8	182.8	0.50	110.7	1.32
10	165.0	0.42	84.2	1.14

for the dynamic demand model. Quantities predicted by Equations (15) and (16) and price elasticities of demand for a range of prices are listed in Table 7. From the Table and Figure 1 it is clear that the two demand models are grossly similar. At low supply levels (less than about 250 t), however, the predicted price responses are greatly different, as are the quantities demanded when prices are low (<\$4 per unit protein). Thus, any conclusions reached on the basis of this demand analysis will be sensitive to the specification of the demand function.

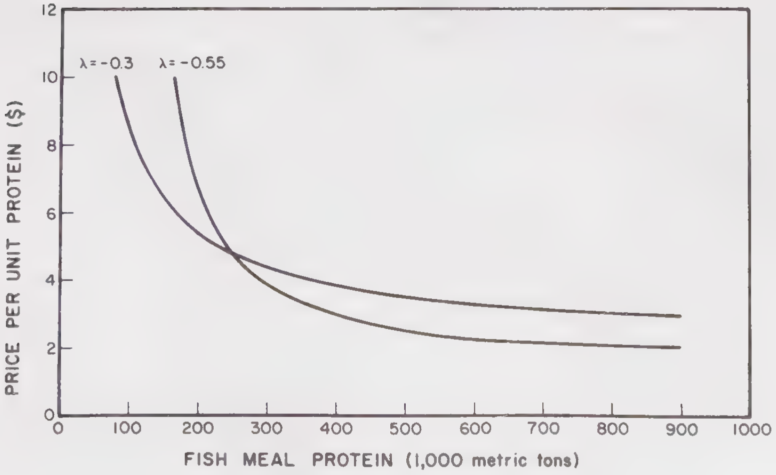

FIGURE 1.—Fish meal demand curves based upon the maximum likelihood estimates of the static demand model ($\lambda = -0.55$) and the partial adjustment model ($\lambda = -0.3$).

Most economic models of fishery management have ignored the influence of landings on the price of fish or fishery products. The assumption of fixed price is a particularly attractive one, because with fixed prices the harvest quantity is proportional to the total revenue. Only the relationship between costs and landings must be added to the model in order to derive economic critertia for optimization. When management programs control landings which are large relative to the market demand, however, the price is likely to become a variable rather than a fixed parameter. The use of demand relationships, such as the one estimated above, will undoubtedly become important as more control is exercised over more fisheries in the United States. The means for incorporating demand analysis into fishery management models is explained by Anderson (1973) and Clark (1976, chapter 5). More extensive use of these complex models which include variable prices will proceed only as fast as the development of solid, empirical demand studies.

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A Comparison of Surface Heat Flux Estimates from Ocean Weather Station V and Merchant Vessels in Its Vicinity in the Western North Pacific Region, 1956–1970

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20 April 1979 and 23 July 1979

ABSTRACT

In this report the estimates of large-scale heat fluxes derived from merchant vessel data within a 4° quadrangle centered on the position of Ocean Weather Station V in the western Pacific Ocean are compared with the estimates from the assumed higher quality weather reports at OWS-V during 1956–70. Comparison of the anomalies of the 6-monthly mean latent heat flux estimates from the long-term means of the two data sets revealed significantly different patterns in the latent heat flux, particularly during the 1956–66 period.

Investigation of the monthly mean properties used to compute the heat flux estimates showed a statistically significant trend in the differences between the sea surface temperatures. The trend in the SST differences is believed to result from the inclusion of low-precision merchant vessel data collected prior to 1962. There is also a suggestion that this trend may have resulted from sampling bias (in terms of data density and bias in location of the observations).

The results indicate that the use of time- and space-averaged properties or heat flux estimates derived from the TDF-11 file requires careful screening of the reports to provide unbiased estimates of air-sea energy transfer processes.

1. Introduction

The increasing research efforts toward understanding the mechanisms of climatic change require knowledge of the air-sea energy transfer processes over large ocean areas. The only source of historical and modern data over large ocean areas which can be used to estimate the energy transfers is the file of surface marine weather observations, collected primarily by merchant vessels, which is archived at the National Climatic Center (NOAA, EDIS) in Tape Data Family-11 (TDF-11). These data have been used in recent climatological summaries of surface heat flux estimates for the eastern North Pacific Ocean by Clark *et al.* (1974) and for the North Atlantic Ocean by Bunker (1976). An important concern is the representativeness of the heat flux estimates derived from the merchant vessel data, given the possible sources of error in these data, such as the nonrandom distribution of the reports, fair weather bias and sampling errors.

Recently some comparisons have been made between long-term means of merchant vessel surface weather data in areas surrounding ocean weather stations and the assumed higher quality ocean weather station (OWS) data. Quayle (1974) investigated the possible fair weather bias in merchant vessel reports by comparing the percentage departures of the monthly mean values in 2° latitude-longitude squares surrounding OWS's with the overall OWS monthly means. He reported that the wind speed comparisons showed no significant differences but that the precipitation and visibility comparisons did show possible avoidance of bad weather, i.e., less precipitation and greater visibility reported by the merchant vessels. Bunker (1976) compared the long-term averages of TDF-11 data within subareas surrounding OWS's with the long-term OWS averages in the North Atlantic. The results indicated that the merchant vessel observers measured higher sea and dew-point temperatures and lower wind speeds and cloud cover than those at OWS D and E. Based on comparisons using more than 500 observations, the probable error in the latent heat flux computations was estimated to be less than 10%.

In this report the time series of 6-monthly and monthly mean estimates of the turbulent heat flux from OWS-V (34°N, 164°E) and the surrounding 4° square are compared for the 1956–70 period. The differences in the patterns of the anomalies of the 6-monthly estimates are described. The objective in comparing the two sets of calculations was to determine whether meaningful anomalies of energy transfer can be computed from the merchant vessel

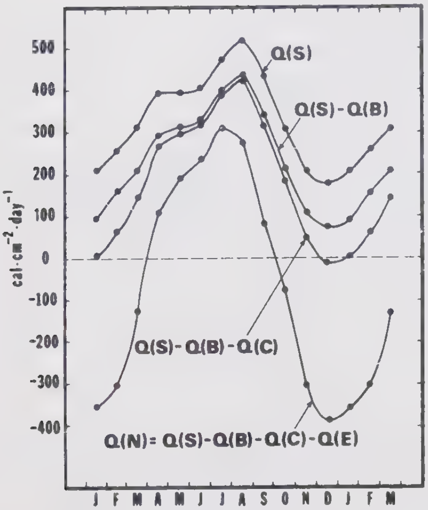

FIG. 1. Mean annual cycle of components of heat exchange across the sea surface at Ocean Weather Station V, 1956–70. $Q(S)$, radiation from sun and sky; $Q(B)$, effective back radiation; $Q(C)$, sensible heat flux; $Q(E)$, latent heat flux; and $Q(N)$, net heat exchange.

data. The factors contributing to differences in the heat flux estimates are discussed.

2. Data processing and heat flux computations

Monthly means of air, sea and dew-point temperatures and wind speed and cloud amounts were calculated from the TDF-11 data for the 4° square surrounding OWS-V and for the 3 h synoptic weather reports from the OWS vessels for the 1956–70 period. The number of observations per month for the 4° square ranged from 21 to over 800, with an average of 120, while for the OWS-V reports the numbers ranged from 137 to 248, with 98% of the months having more than 200 observations. Gross error checking was performed on each report to determine only if the reported values were within normal climatic limits.

TABLE 1. Six-monthly heat exchange processes, 1956–70 (cal cm^{-2} day^{-1}).

	October–March		April–September	
	4° square	OWS-V	4° square	OWS-V
$Q(S)$	285	238	497	429
$Q(B)$	−110	−106	−91	−86
$Q(C)$	−74	−70	−11	−13
$Q(E)$	−328	−329	−152	−137
$Q(N)$	−227	−267	243	193

$Q(S)$, incident solar radiation: $Q(B)$, effective back radiation: $Q(C)$, sensible heat flux: $Q(E)$, latent heat flux: $Q(N)$, net heat exchange.

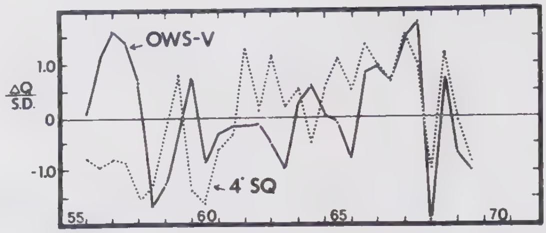

FIG. 2. Time series of standardized anomalies of 6-monthly latent heat flux at OWS-V (solid line) and within 4° square surrounding OWS-V (dashed line). The two 6-monthly periods are October–March and April–September.

The energy transfer processes, that is, the turbulent fluxes of latent and sensible heat and the effective back radiation from the sea surface, were estimated using the standard bulk exchange formulas with a constant drag coefficient referred to the 10 m reference height. The formulas are described in Husby and Seckel (1975). The identical formulas were used with the monthly mean properties from both sets of data. Although the heights of the wind speed observations and that for the air and dew-point temperatures were different for both the OWS vessels and the merchant vessels, the anemometer heights on the merchant vessels cannot be determined. Thus, the heat flux computations were performed using the original observations, unadjusted for the difference in heights, and the drag coefficient for the 10 m reference height.

3. Anomalies of latent heat flux

During the months from October through March there is a net loss of heat from the ocean to the atmosphere at OWS-V which averages 267 cal cm^{-2} day^{-1} (129 W m^{-2}) and during the April to September months the ocean gains an average of 193 cal cm^{-2} day^{-1} (92 W m^{-2}) (Fig. 1). The latent heat flux $Q(E)$ is the largest term contributing to the annual cycle of heat exchange aside from the solar radiation $Q(S)$ reaching the sea surface, particularly during the cooling portion of the annual cycle from October to March. Table 1 lists the 15-year means from the two sets of data for the terms comprising the net heat exchange during the two 6-month portions of the annual cycle. There was very little difference in the long-term means of the 6-month estimates of the heat flux terms. The differences arise when the anomalies of the 6-month means from the long-term averages of both data sets are examined.

Fig. 2 displays the anomalies (deviations from the respective long-term 6-month means) of the latent heat flux estimates for the two data sets for the two 6-month segments of the annual cycle. The positive anomalies denote greater than average latent heat flux from the ocean to the atmosphere and the nega-

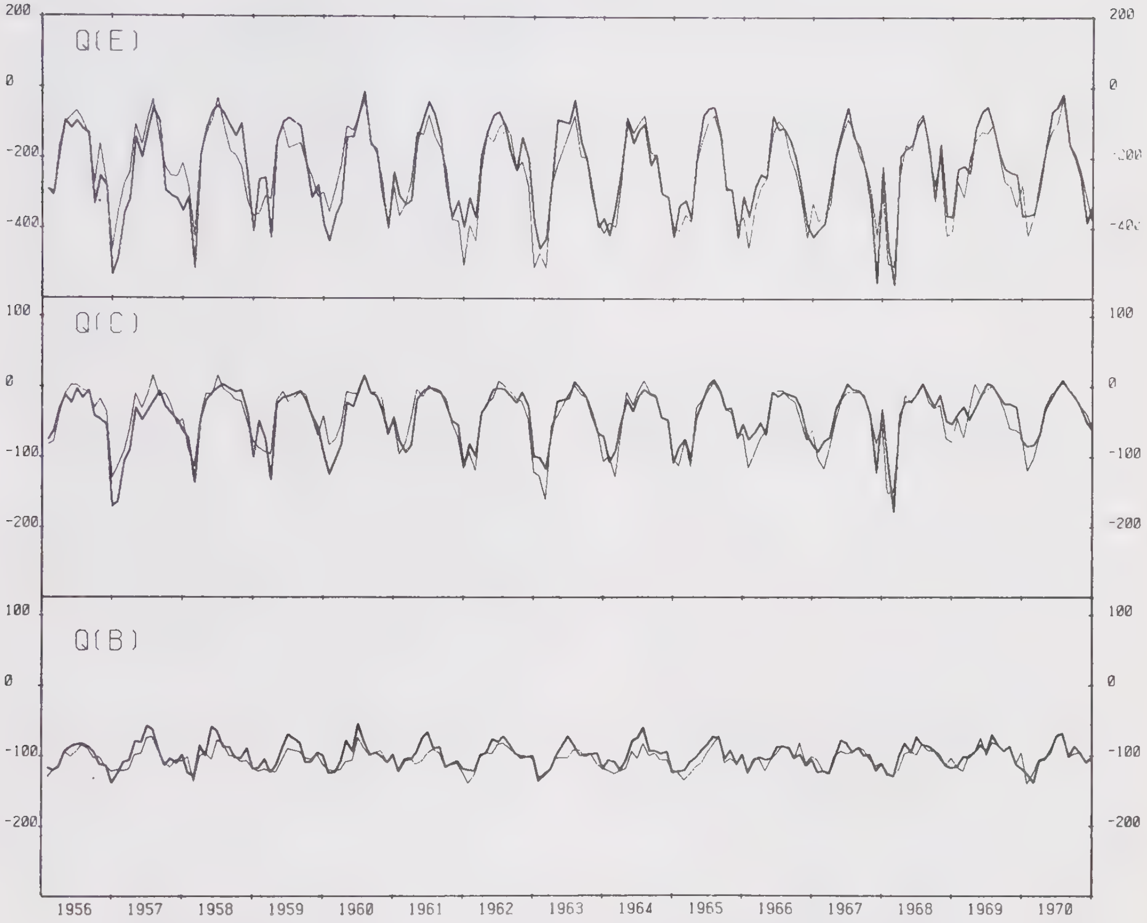

Fig. 3. Time series of monthly latent heat flux (upper panel), sensible heat flux (middle panel), and effective back radiation (bottom panel) at OWS-V (heavy lines) and within 4° square surrounding OWS-V (light lines). Units are cal cm^{-2} day^{-1}.

tive anomalies less than average latent heat flux. The anomalies are transformed into standardized variables by dividing the anomaly value by the standard deviation of the 6-month anomalies for the 15-year period. Prior to 1966 the 6-month anomalies based on the 4° square data are radically different from the OWS-V 6-month anomalies. Large differences are evident during the 1956–58 period. Also noted are the large, positive anomalies in the TDF-11 data for October 61–March 62, October 62–March 63, April 65–September 65 and April 66–September 66. The differences between the individual 4° square and the OWS-V 6-month means were of the same magnitude as the 6-month anomalies of the OWS-V values.

The differences in the patterns of the 6-month anomalies of the latent heat flux are readily explained in the comparison of the monthly values (Fig. 3). Particularly during the winter months from 1956 to 1963, the latent heat flux estimates derived from the TDF-11 data seem to be consistently biased compared to the OWS-V values. There are periods of 3–6 months in succession when the $Q(E)$ values are consistently less or greater than those derived from the OWS-V data. During the winters of 1956–57, 1957–58 and 1959–60 the 4° square $Q(E)$ estimates were consistently less than those for the OWS-V data and during the winters of 1961–62 and 1962–63, the reverse was true. Hishida and Nishiyama (1969) noted a long-term trend in the monthly anomalies of latent heat flux over a large portion of the western North Pacific Ocean during the 1954–63 period based on the marine climatological tables of the Japan Meteorological Agency. The monthly anomalies in latent heat flux in selected 2° × 5° latitude-longitude quadrangles were predominantly negative in the 1954–59 period and positive from 1960–63. The authors suggested that the

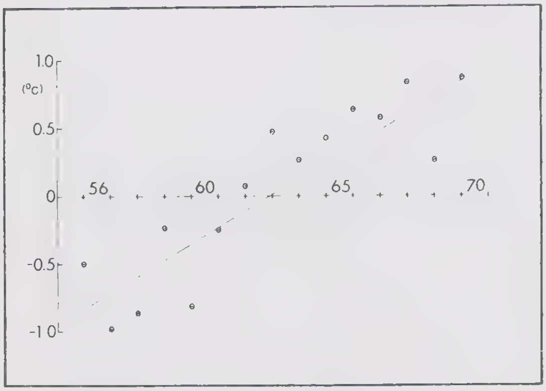

FIG. 4. Difference in October to March mean sea surface temperature between 4° square surrounding OWS-V and OWS-V. Straight line indicates linear regression of temperature difference on the year.

anomalies in the evaporation rate were related to anomalies in the wind speed, particularly in January and February.

4. Comparison of monthly mean meteorological properties

To investigate these non-random differences in the $Q(E)$ estimates, monthly mean values of sea surface temperature, air temperature, wind speed and vapor pressure of the air were compared. The Mann-Kendall rank statistic was computed for each series of differences to test the series for randomness versus the alternative hypothesis of a trend (Mitchell *et al.*, 1966). Only the sea surface temperature (SST) differences showed the probability of a trend, significant at the 95% level. Fig. 4 displays the differences in the October–March mean SST values for the 1956–70 period. The differences range from about −1°C in 1957 to +1°C in 1970.

The Behrens-Fisher statistic was computed to test the hypothesis that there was no difference between the monthly SST means (Fisher and Yates, 1970). The hypothesis could be rejected for only 40% of the months in this comparison; however, nearly 50% of the comparisons for the October–March months produced differences which were significantly greater than zero at the 95% level. A possible cause for the disagreement in the SST monthly means is the inclusion of low-precision SST values in the TDF-11 file for the 1956–61 period.

From 1956 to 1961 nearly 50% of the reports were derived from Deck 119, Japanese Ship Observations (Fig. 5). The SST values in Deck 119 were calculated from the difference between the reported air-sea temperature difference and the reported air temperature which are given to the nearest whole degree Celsius. Thus these SST values contain an uncertainty of ±0.5°C in addition to other sampling errors. The other decks contributing to the 4° square data contained SST values reported to the nearest tenth of a degree Celsius. Uncertainties in the SST means alone of 0.5–1.0°C could produce uncertainties in the latent heat flux estimates of 10–20%. However, correcting the monthly SST values for the linear trend did not significantly alter the differences in the latent heat flux estimates.

The mean wind speeds, air temperatures and vapor pressures of the air were generally higher for the 4° square data than for the OWS-V reports although no significant trends were detected; the root-mean-square (rms) differences were 1.0 m s^{-1}, 0.5°C and 0.9 mb, respectively. The magnitudes of the sampling errors of the individual merchant vessel and OWS measurements cannot be determined due to the variety of methods and instruments used; however, considerable variation in the mean properties is expected *a priori* due to the errors in interpolating the mean property within the 4° square to the midpoint of the area. The 4° square means may be biased toward certain shipping lanes and possibly toward a certain time period during the month.

The spatial bias in the monthly mean properties was examined by calculating the rms distances of the 4° square reports from the position of OWS-V for the individual months. The rms distances did not show any appreciable changes or trends from month-to-month, but were relatively constant at about 0.6° latitude (~67 km). However, there was a slight trend in the monthly mean location of the 4° square reports which consisted of a decrease in the mean latitude of the reports of 0.5° latitude from

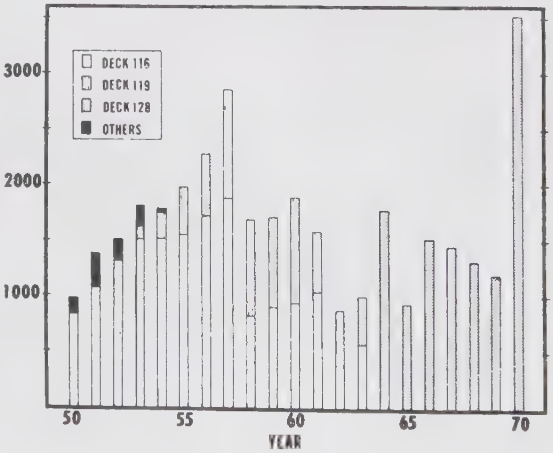

FIG. 5. Annual number of reports within the 4° square surrounding OWS-V and the source of the reports within each year. Deck 116, U.S. Merchant Marine observations; Deck 119, Japanese Ship Observations No. 2; and Deck 128, International Marine Observations.

1956 to 1970. The magnitude of this trend was not sufficient to explain the trend in the sea surface temperatures mentioned earlier. The sea surface temperature gradients are primarily meridional in the vicinity of OWS-V throughout the year and, based on historical oceanographic data, the gradients range from 0.4°C per degree latitude in the summer to 0.9°C per degree latitude in the winter (Japan Oceanographic Data Center, 1975).

5. Summary

The record of climatic-scale fluctuations in the upper ocean must presently depend on the routinely collected surface weather observations from merchant vessels. An important component of the energy budget of the ocean is the turbulent transfer of energy between the atmosphere and ocean. The anomalies of the 6-month latent heat flux means from the long-term (15-year) average for the two data sets did not show good agreement in the winter months (October–March) for the 1956–66 period. In fact, the anomalies were of different sign during 1956–58, 1963 and 1965–66.

The discrepancies in the 6-monthly and monthly estimates of latent heat flux appear to be primarily related to the inclusion of low-precision data in the time series of sea surface temperature reports in the TDF-11 file during the 1956–61 period. A slight negative trend in the mean latitude of the TDF-11 reports was identified which, by itself, was not sufficient to explain the differences in the monthly mean properties or the derived heat flux estimates.

The pitfalls in using the bulk aerodynamic formulas with a constant drag coefficient and with monthly mean properties have been discussed by many investigators. The calculation of the turbulent energy transfers with the bulk formulas is usually made with the intention of providing relative indices of the month-to-month or interannual variations in the energy transfers rather than determining the absolute magnitudes of the processes. The results of this comparison throw some doubt on the use of the merchant vessel data even for relative indices of air-sea interaction at least in this portion of the western North Pacific. The poor comparisons of the heat flux anomalies underscore the need for careful screening of the merchant vessel reports prior to the heat flux computations.

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Table 4. Monthly mean sea-surface temperature anomalies (°C) from the 1948–1967 monthly means for 1978 in the northwestern Atlantic Ocean (35°–46°N 60°–76°W)

Month	Number of 1° squares	Area mean anomaly	Standard deviation of area mean anomalies in 1948-1967
Jan	101	-0·29	1·26
Feb	120	-0·80	1·23
Mar	115	-0·75	1·49
Apr	125	-0·47	1·51
May	126	-0·45	1·22
Jun	129	-0·03	0·91
Jul	119	-0·38	0·89
Aug	117	+ 0·36	0·85
Sep	109	0·03	0·89
Oct	117	-0·44	0·95
Nov	112	+ 0·07	0·90
Dec	112	+ 0·29	0·91

Sea-surface temperatures in the northwestern Atlantic in 1978

(Figures 43-58; Table 4)

Water temperature data, principally collected from cooling water intakes of merchant ships, are reported in radio weather messages and log books transmitted to the U.S. Fleet Numerical Weather Central (FNWC) and the National Climatic Center for processing and archiving. The "real-time" reports of the data base provided by the radio messages are analysed by FNWC and the Pacific Environmental Group of the National Marine Fisheries Service, which is co-located with FNWC. An elementary step in the analysis is the computation of average monthly temperatures and anomalies (from 1948-1967 means) for each 1° × 1° square for which enough data have been reported each month. The average temperatures, anomalies, and number of observations are then printed in the 1° × 1° squares they characterize to produce maps such as those shown in Figures 43-54. To facilitate interpretation of the data, anomalies greater than + 1°C or less than -1°C are shaded.

Monthly maps of this sort for the northwestern Atlantic for 1978 (Figs. 43-54) reveal that sea-surface temperatures in the area generally were cooler than the long-term (1948-1967) mean during the first half of the year. Extensive areas of negative anomalies as great as -7·7°C developed, with the most extensive and intensive occurring in February. The anomalies were generally stronger in the southwest corner of the area, but the cold water extended farthest eastward off the Middle Atlantic Bight and southern New England (38°-41°N).

In an effort to characterize sea-surface temperature in the entire area (35°-46°N 60°-76°W) with a single number, the mean of all the mapped anomalies was computed for each month. The resulting monthly area

Figures 43-54. Average sea-surface temperature anomalies (°C). Also shown in each 1° square are average sea-surface temperatures (upper number) and the number of observations (lower number).

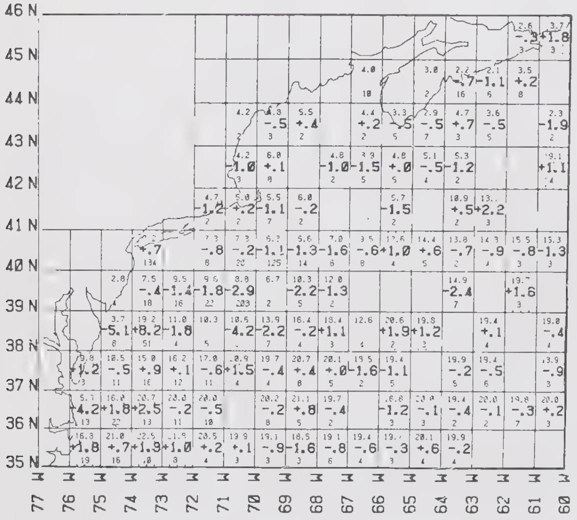
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Figure 43. January 1978.

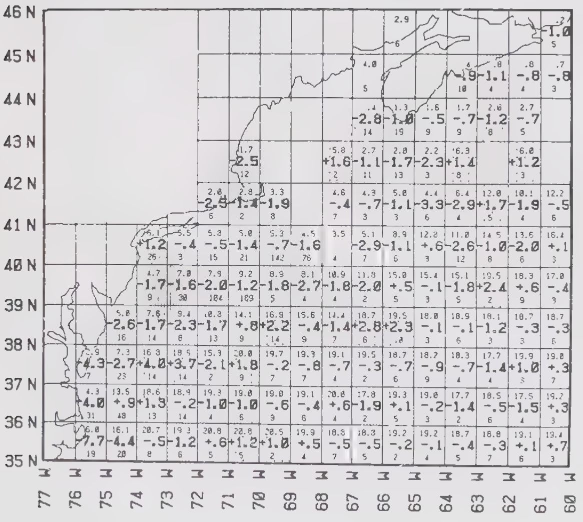
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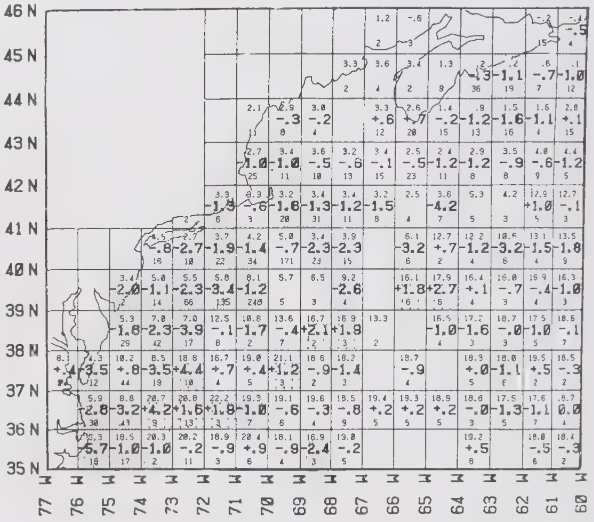
Figure 44. February 1978.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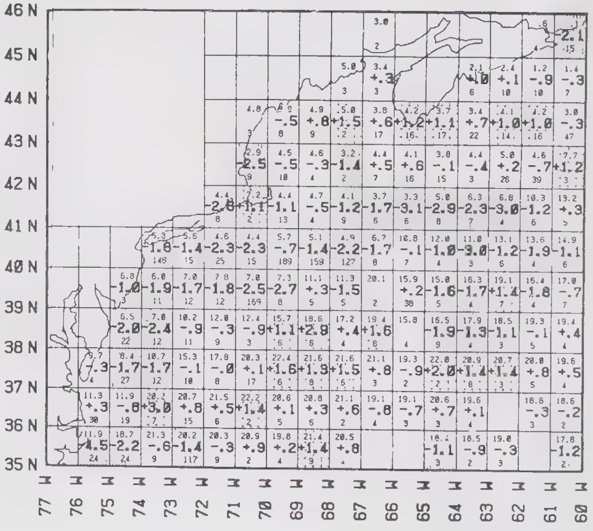
77 76 75 74 73 72 71 70 69 68 67 66 65 64 63 62 61 60

Figure 45. March 1978.


46 N
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37 N
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35 N
77 76 75 74 73 72 71 70 69 68 67 66 65 64 63 62 61 60

Figure 46. April 1978.

means (Table 4) show negative values for all months except August, November, and December. However, the magnitudes of the negative area anomalies are significantly less than the standard deviation of the area anomalies for the reference period (1948-1967) as shown in Table 4. Apparently the negative anomalies in 1978 were not unusually intense, even though they were widespread and persistent.

In order to characterize the spatial and temporal gradients in shelf waters during the course of 1978, monthly anomalies from 15 one-degree squares (Fig. 55) were plotted on a space-time grid (Fig. 56). The plot clearly shows that the shelf water exhibited the greatest negative anomalies in the late winter and spring months (February-May) and in the area off Delaware Bay-Cape Hatteras (squares 12-15). In the

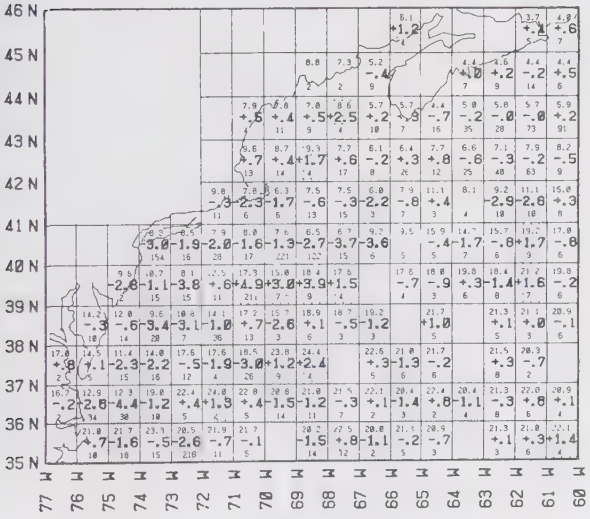
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Figure 47. May 1978.

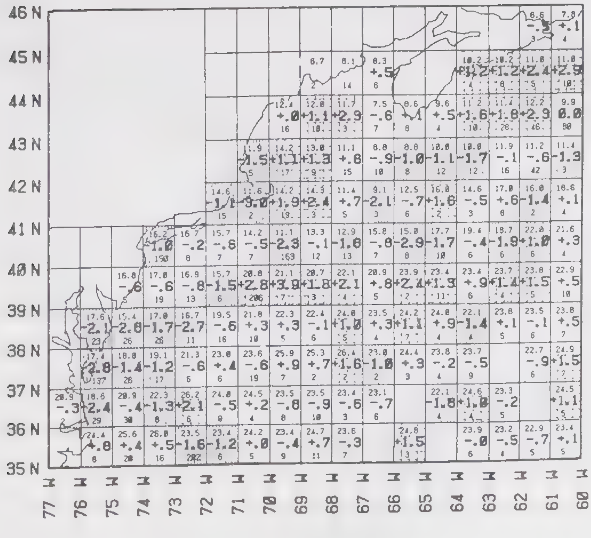
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Figure 48. June 1978.

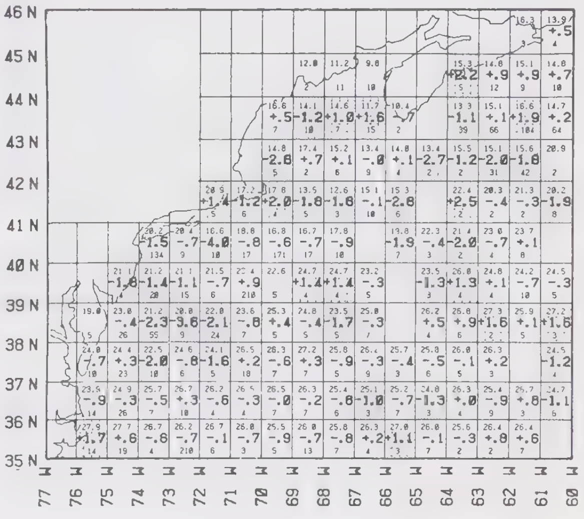
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Figure 49. July 1978.

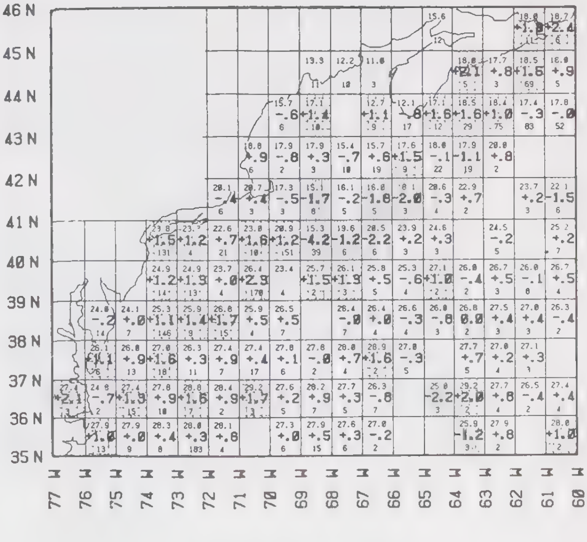
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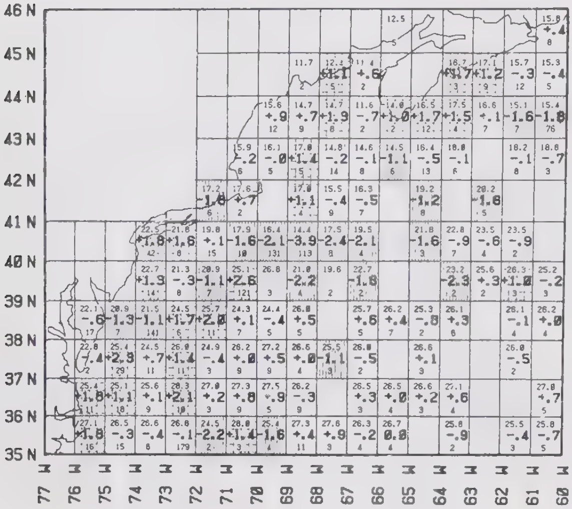
Figure 50. August 1978.

New York Bight, however, (squares 9, 10, and 11) the negative anomalies were smaller and developed later in the year. Off southern New England (squares, 6, 7, and 8) the negative anomalies developed early, in the winter months, but were smaller in general than those in the southern squares. On Georges Bank (squares 4 and 5) development of negative anomalies was weak and sporadic. The Scotian Shelf (squares 1, 2, and 3) showed no strong anomaly patterns, neither negative nor positive.

In 1977 (Fig. 57), by comparison, negative anomalies in shelf waters appeared earlier, being widespread in January (and December 1976). However, they weakened earlier, and by May only two squares showed values stronger than -1°C. By June strong positive anomalies had developed off New Jersey-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74 W
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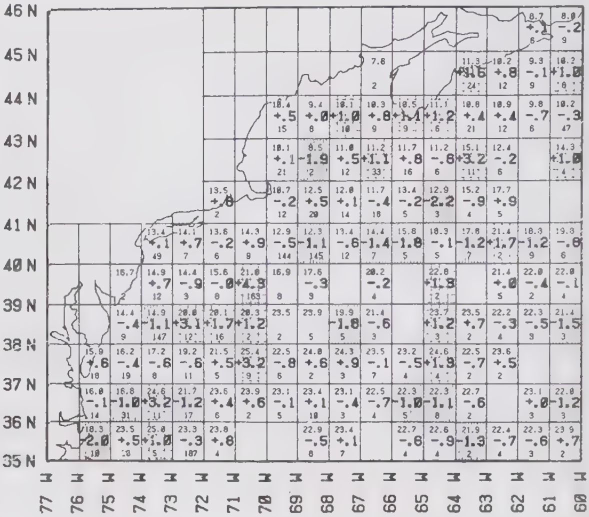
66 W
65 W
64 W
63 W
62 W
61 W
60 W

Figure 51. September 1978.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41 N
40 N
39 N
38 N
37 N
36 N
35 N
77 W
76 W
75 W
74 W
73 W
72 W
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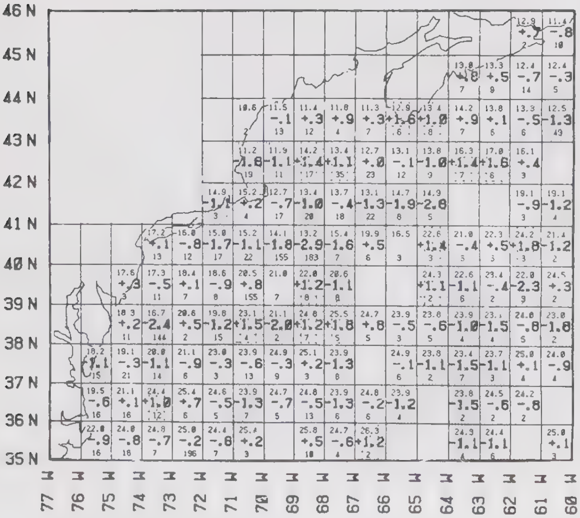
70 W
69 W
68 W
67 W
66 W
65 W
64 W
63 W
62 W
61 W
60 W

Figure 53. November 1978.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37 N
36 N
35 N
77 W
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75 W
74 W
73 W
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68 W
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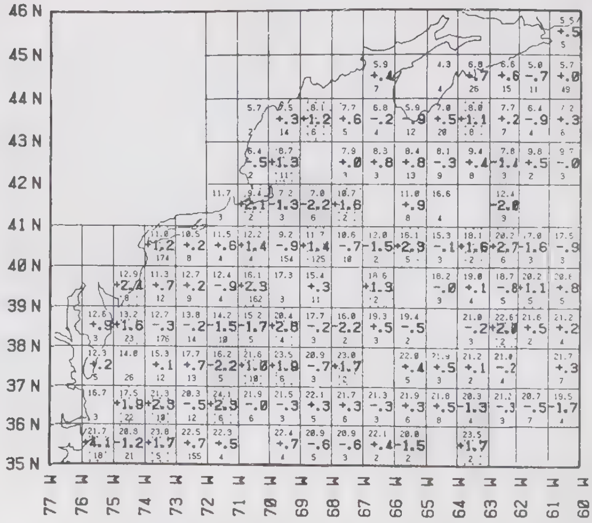
66 W
65 W
64 W
63 W
62 W
61 W
60 W

Figure 52. October 1978.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37 N
36 N
35 N
77 W
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75 W
74 W
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64 W
63 W
62 W
61 W
60 W

Figure 54. December 1978.

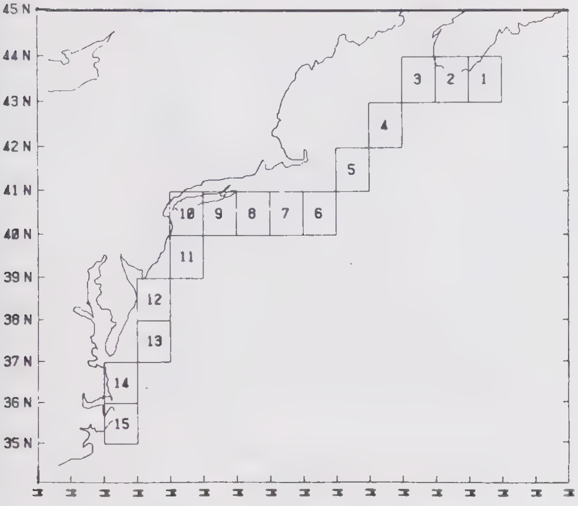
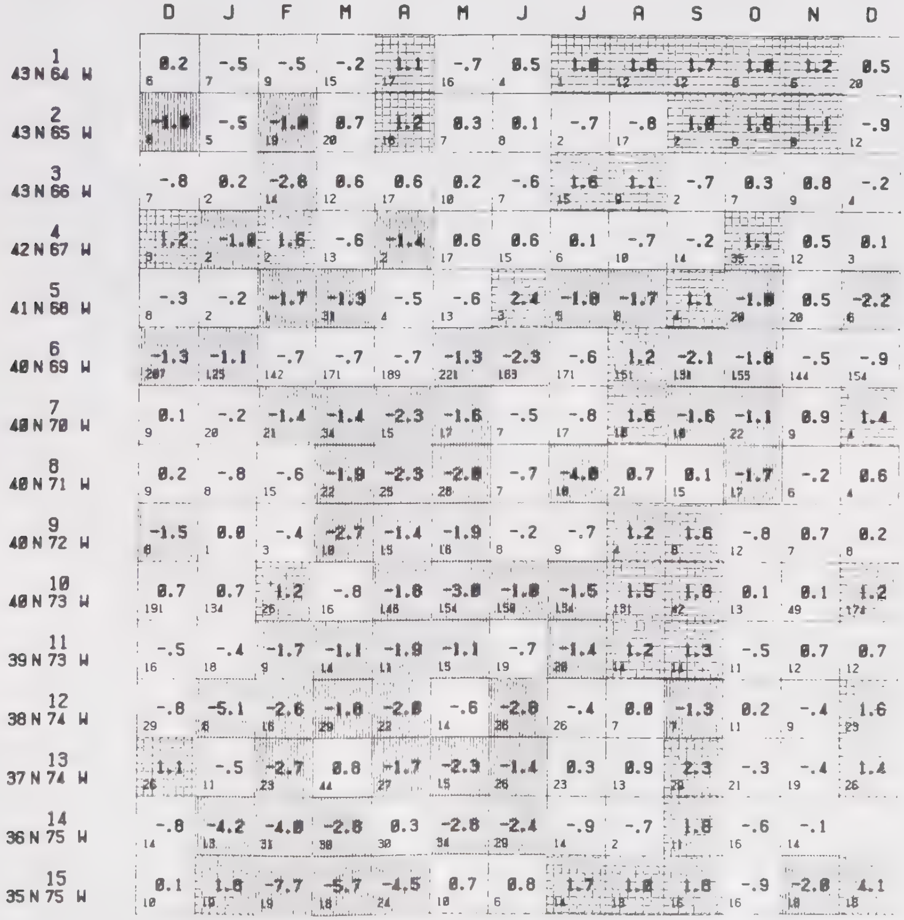


Figure 55 (left). Location of 1° squares of interest utilized in Figures 56 58.

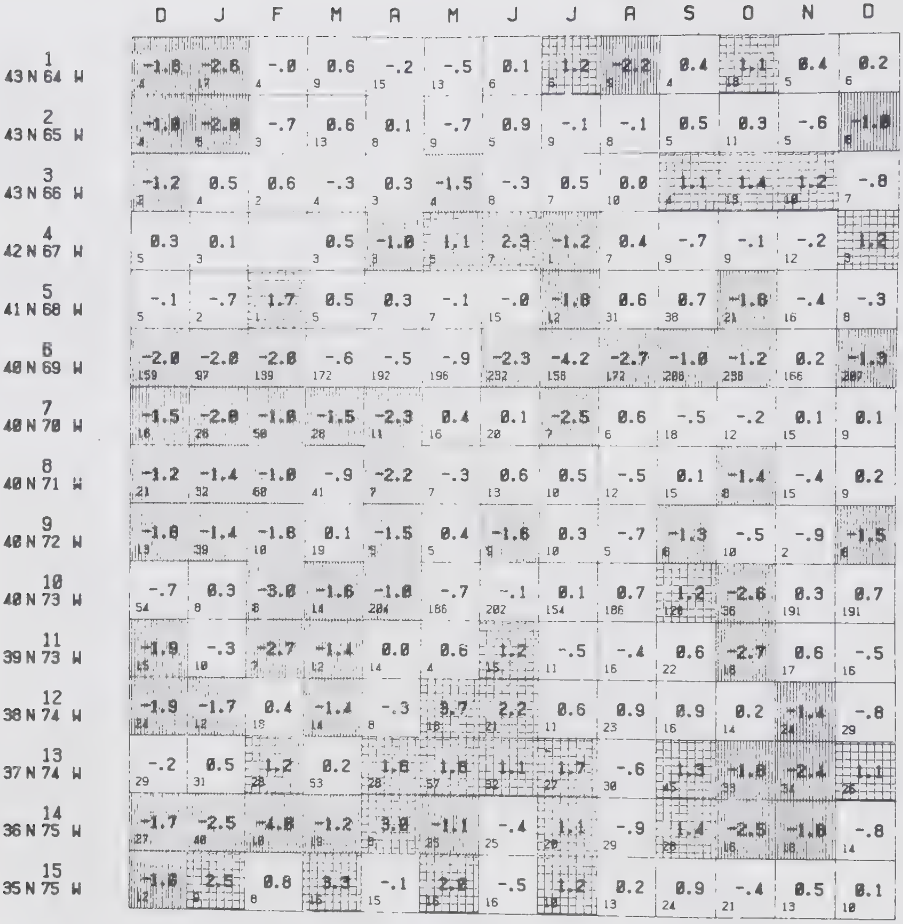
Virginia (squares 11-13). Geographically, the pattern in 1977 was somewhat similar to 1978, with the negative anomalies extending from southern New England to Cape Hatteras (squares 6-15) and the most intense anomalies occurring at the southern end of the region (square 14) off Virginia-North Carolina.

The previous year, 1976 (Fig. 58), did not show an extensive pattern of negative anomalies in the early months of the year. In fact, no significant areal pattern developed until late summer and fall (August-December). In the northern section, on Georges Bank

Figure 56 (below). Space-time plot of monthly sea-surface temperature anomalies for 1978. Also shown are the numbers of observations utilized (lower left corner of squares).



	D	J	F	M	A	M	J	J	A	S	O	N	D
1 43 N 64 W	0.2 6	-.5 7	-.5 9	-.2 15	1.1 17	-.7 16	0.5 4	1.0 1	1.6 12	1.7 12	1.0 8	1.2 5	0.5 20
2 43 N 65 W	-1.0 8	-.5 5	-1.0 19	0.7 20	1.2 16	0.3 7	0.1 8	-.7 2	-.8 17	1.0 2	1.6 8	1.1 9	-.9 12
3 43 N 66 W	-.8 7	0.2 2	-2.8 14	0.6 12	0.6 17	0.2 10	-.6 7	1.6 15	1.1 9	-.7 2	0.3 7	0.8 9	-.2 4
4 42 N 67 W	1.2 3	-1.0 2	1.6 2	-.6 13	-1.4 2	0.6 17	0.6 15	0.1 6	-.7 10	-.2 14	1.1 35	0.5 12	0.1 3
5 41 N 68 W	-.3 8	-.2 2	-1.7 4	-1.3 31	-.5 4	-.6 13	2.4 3	-1.0 5	-1.7 8	1.1 4	-1.0 20	0.5 20	-2.2 6
6 40 N 69 W	-1.3 207	-1.1 125	-.7 142	-.7 171	-.7 189	-1.3 221	-2.3 183	-.6 171	1.2 151	-2.1 191	-1.0 155	-.5 144	-.9 154
7 40 N 70 W	0.1 9	-.2 20	-1.4 21	-1.4 34	-2.3 15	-1.6 17	-.5 7	-.8 17	1.6 18	-1.6 10	-1.1 22	0.9 9	1.4 4
8 40 N 71 W	0.2 9	-.8 8	-.6 15	-1.9 22	-2.3 25	-2.0 28	-.7 7	-4.0 10	0.7 21	0.1 15	-1.7 17	-.2 6	0.6 4
9 40 N 72 W	-1.5 8	0.0 1	-.4 3	-2.7 10	-1.4 15	-1.9 18	-.2 8	-.7 9	1.2 4	1.6 8	-.8 12	0.7 7	0.2 8
10 40 N 73 W	0.7 191	0.7 134	1.2 26	-.8 16	-1.8 148	-3.0 154	-1.0 150	-1.5 134	1.5 131	1.8 42	0.1 13	0.1 49	1.2 174
11 39 N 73 W	-.5 16	-.4 18	-1.7 9	-1.1 14	-1.9 11	-1.1 15	-.7 19	-1.4 20	1.2 11	1.3 11	-.5 11	0.7 12	0.7 12
12 38 N 74 W	-.8 29	-5.1 6	-2.6 16	-1.0 29	-2.0 22	-.6 14	-2.8 28	-.4 26	0.0 7	-1.3 7	0.2 11	-.4 9	1.6 29
13 37 N 74 W	1.1 26	-.5 11	-2.7 23	0.8 44	-1.7 27	-2.3 15	-1.4 26	0.3 23	0.9 13	2.3 29	-.3 21	-.4 19	1.4 26
14 36 N 75 W	-.8 14	-4.2 13	-4.0 31	-2.8 38	0.3 30	-2.8 34	-2.4 28	-.9 14	-.7 2	1.8 11	-.6 16	-.1 14	
15 35 N 75 W	0.1 10	1.8 19	-7.7 19	-5.7 18	-4.5 24	0.7 10	0.8 6	1.7 14	1.8 18	1.8 16	-.9 16	-2.0 10	4.1 18



	D	J	F	M	A	M	J	J	A	S	O	N	D
1 43 N 64 W	-1.8 4	-2.6 17	-.0 4	0.6 9	-.2 15	-.5 13	0.1 6	1.2 6	-2.2 9	0.4 4	1.1 18	0.4 5	0.2 6
2 43 N 65 W	-1.0 4	-2.0 5	-.7 3	0.6 13	0.1 8	-.7 9	0.9 5	-.1 9	-.1 8	0.5 5	0.3 11	-.6 5	-1.8 6
3 43 N 66 W	-1.2 2	0.5 4	0.6 2	-.3 4	0.3 3	-1.5 4	-.3 8	0.5 7	0.0 10	1.1 4	1.4 15	1.2 10	-.8 7
4 42 N 67 W	0.3 5	0.1 3		0.5 3	-1.0 3	1.1 5	2.3 7	-1.2 1	0.4 7	-.7 9	-.1 9	-.2 12	1.2 3
5 41 N 68 W	-.1 5	-.7 2	1.7 1	0.5 5	0.3 7	-.1 7	-.0 15	-1.0 12	0.6 31	0.7 38	-1.8 21	-.4 16	-.3 8
6 40 N 69 W	-2.0 159	-2.0 97	-2.0 139	-.6 172	-.5 192	-.9 196	-2.3 282	-4.2 158	-2.7 172	-1.0 208	-1.2 238	0.2 166	-1.3 207
7 40 N 70 W	-1.5 16	-2.0 26	-1.0 50	-1.5 28	-2.3 11	0.4 16	0.1 20	-2.5 7	0.6 6	-.5 18	-.2 12	0.1 15	0.1 9
8 40 N 71 W	-1.2 21	-1.4 32	-1.0 68	-.9 41	-2.2 7	-.3 7	0.6 13	0.5 10	-.5 12	0.1 15	-1.4 8	-.4 15	0.2 9
9 40 N 72 W	-1.0 13	-1.4 39	-1.8 10	0.1 19	-1.5 5	0.4 5	-1.6 9	0.3 10	-.7 5	-1.3 6	-.5 10	-.9 2	-1.5 6
10 40 N 73 W	-.7 54	0.3 8	-3.0 8	-1.6 14	-1.0 204	-.7 186	-.1 202	0.1 154	0.7 186	1.2 120	-2.6 36	0.3 191	0.7 191
11 39 N 73 W	-1.9 15	-.3 10	-2.7 7	-1.4 12	0.0 14	0.6 4	1.2 15	-.5 11	-.4 16	0.6 22	-2.7 18	0.6 17	-.5 16
12 38 N 74 W	-1.9 24	-1.7 12	0.4 18	-1.4 14	-.3 8	3.7 18	2.2 21	0.6 11	0.9 23	0.9 16	0.2 14	-1.4 24	-.8 29
13 37 N 74 W	-.2 29	0.5 31	1.2 28	0.2 53	1.6 28	1.8 57	1.1 32	1.7 27	-.6 30	1.3 45	-1.8 33	-2.4 34	1.1 26
14 36 N 75 W	-1.7 27	-2.5 40	-4.8 10	-1.2 19	3.0 5	-1.1 26	-.4 25	1.1 20	-.9 29	1.4 28	-2.5 16	-1.8 18	-.8 14
15 35 N 75 W	-1.6 12	2.5 5	0.8 8	3.3 16	-.1 15	2.8 15	-.5 16	1.2 10	0.2 13	0.9 24	-.4 21	0.5 13	0.1 10

Figure 57. Space-time plot of monthly sea-surface temperature anomalies for 1977. Also shown are the numbers of observations utilized (lower left corner of squares).

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and the Scotian Shelf, a pattern of strong positive anomalies developed in the spring and summer months. This sort of positive anomaly pattern did not develop during the following two years (1977, 1978).

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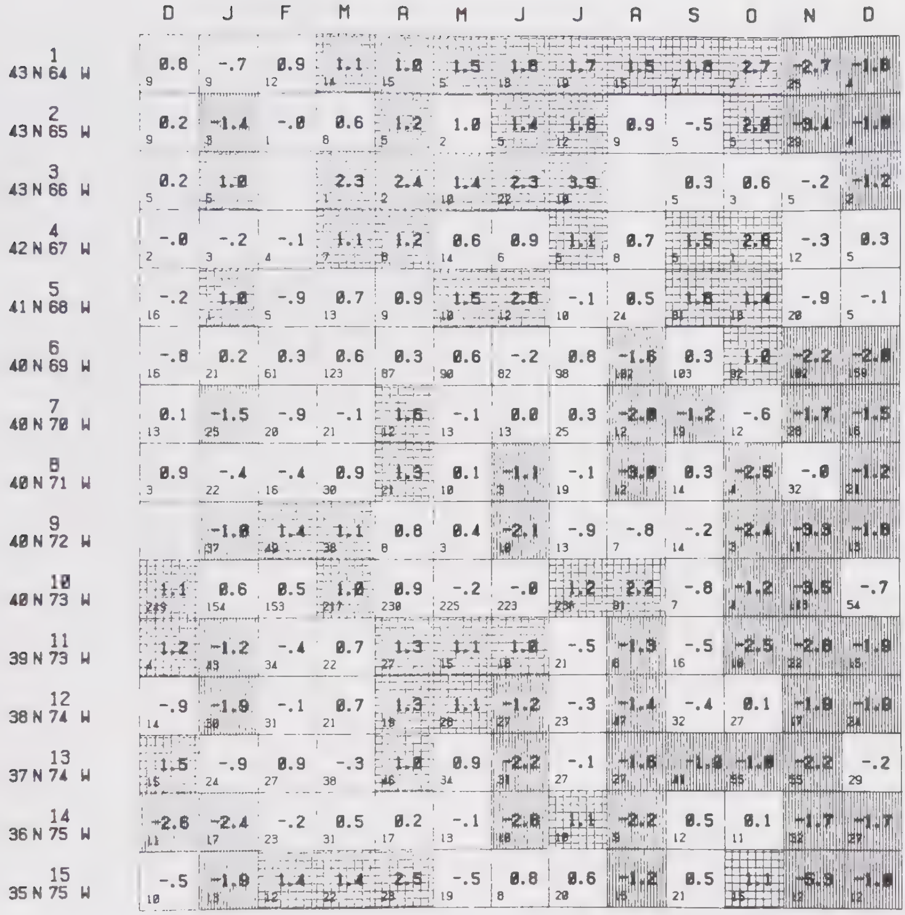
c/o Fleet Numerical Weather Central,
Monterey, California 93940, USA



	D	J	F	M	A	M	J	J	A	S	O	N	D
1 43 N 64 W	0.8 9	-.7 9	0.9 12	1.1 14	1.0 15	1.5 5	1.8 18	1.7 19	1.5 15	1.8 7	2.7 7	-2.7 25	-1.8 4
2 43 N 65 W	0.2 9	-1.4 3	-.0 1	0.6 8	1.2 5	1.0 2	1.4 5	1.6 12	0.9 9	-.5 5	2.0 5	-3.4 29	-1.0 4
3 43 N 66 W	0.2 5	1.0 5		2.3 1	2.4 2	1.4 10	2.3 22	3.9 10		0.3 5	0.6 3	-.2 5	-1.2 2
4 42 N 67 W	-.0 2	-.2 3	-.1 4	1.1 7	1.2 8	0.6 14	0.9 6	1.1 5	0.7 8	1.5 5	2.8 1	-.3 12	0.3 5
5 41 N 68 W	-.2 16	1.0 1	-.9 5	0.7 13	0.9 9	1.5 10	2.6 12	-.1 10	0.5 24	1.6 31	1.4 18	-.9 20	-.1 5
6 40 N 69 W	-.8 16	0.2 21	0.3 61	0.6 123	0.3 87	0.6 90	-.2 82	0.8 98	-1.6 102	0.3 103	1.0 92	-2.2 102	-2.0 159
7 40 N 70 W	0.1 13	-1.5 25	-.9 20	-.1 21	1.6 12	-.1 13	0.0 13	0.3 25	-2.0 12	-1.2 19	-.6 12	-1.7 20	-1.5 16
8 40 N 71 W	0.9 3	-.4 22	-.4 16	0.9 30	1.3 21	0.1 10	-1.1 3	-.1 19	-3.0 12	0.3 14	-2.5 4	-.0 32	-1.2 21
9 40 N 72 W		-1.0 37	1.4 49	1.1 38	0.8 8	0.4 3	-2.1 10	-.9 13	-.8 7	-.2 14	-2.4 3	-3.3 11	-1.8 13
10 40 N 73 W	1.1 249	0.6 154	0.5 153	1.0 217	0.9 230	-.2 225	-.0 223	1.2 234	2.2 91	-.8 7	-1.2 4	-3.5 183	-.7 54
11 39 N 73 W	1.2 4	-1.2 43	-.4 34	0.7 22	1.3 27	1.1 15	1.0 18	-.5 21	-1.3 6	-.5 16	-2.5 10	-2.8 22	-1.9 15
12 38 N 74 W	-.9 14	-1.9 30	-.1 31	0.7 21	1.3 18	1.1 20	-1.2 27	-.3 23	-1.4 47	-.4 32	0.1 27	-1.8 17	-1.8 24
13 37 N 74 W	1.5 15	-.9 24	0.9 27	-.3 38	1.0 46	0.9 34	-2.2 31	-.1 27	-1.6 27	-1.8 41	-1.8 55	-2.2 55	-.2 29
14 36 N 75 W	-2.6 11	-2.4 17	-.2 23	0.5 31	0.2 17	-.1 13	-2.6 10	1.1 10	-2.2 9	0.5 12	0.1 11	-1.7 52	-1.7 27
15 35 N 75 W	-.5 10	-1.9 13	1.4 12	1.4 22	2.5 23	-.5 19	0.8 8	0.6 20	-1.2 16	0.5 21	1.1 15	-5.3 12	-1.8 12

Figure 58. Space-time plot of monthly sea-surface temperature anomalies for 1976. Also shown are the numbers of observations utilized (lower left corner of squares).

8042

EXECUTIVE SUMMARY

Merton C. Ingham[1] and Douglas R. McLain[2]

During the winters of 1976-77 and 1977-78 a strong and persistent ridge of upper air circulation occurred over the west coast of North America from California to Alaska. This ridge brought southerly winds and mild temperatures to much of the coast. In Alaska the mild temperatures broke the period of abnormal cold of the early 1970's and allowed a remarkable recovery of salmon stocks.

During the 15-month period January 1978-March 1979, the upper air circulation over the northeastern Pacific Ocean shifted from the west coast ridge pattern of the previous two years and appeared to be returning to a more normal pattern. The west coast ridge reoccurred during the early part of the winter of 1978-79, but by the end of the winter it had shifted westward and weakened.

The pattern of anomaly of sea-surface temperature (SST) over the northeastern North Pacific shifted in association with the shifting pattern of atmospheric circulation. Whereas anomalies of SST had been generally negative in the central North Pacific and zero or positive near the west coast in 1977 and early 1978, in late 1978 and early 1979 the pattern shifted to one of positive anomalies in a large region between Hawaii and Alaska with negative anomalies all along the west coast. Whether this shift is truly indicative of a change from the pattern of the previous two years or not remains to be seen, because in summer 1979, after the end of the 15-month analysis period, the pattern of SST anomalies had reverted to the prevailing pattern of cold in the central North Pacific and warm along the eastern shore of the ocean.

The wind-driven surface ocean transport during January 1978-March 1979 was abnormal in several biologically important ways. During late 1977 and early 1978 strong northeastward transport occurred in the Gulf of Alaska and along the British Columbia coast. The resulting onshore transport resulted in an intrusion of southern, pelagic fauna into the area, and caused a large percentage of adult Fraser River sockeye salmon to return to the river through Queen Charlotte Sound rather than via the Strait of Juan de Fuca.

Off California, winter onshore transport was much stronger than normal during January-March 1978 and, to a lesser extent, again in December 1978-January 1979 and in March 1979. These strong onshore transports resulted in downwelling and thus extremely low computed indices of upwelling. The onshore transport held larvae of pelagic spawners such as anchovy and Pacific mackerel near shore and apparently resulted in better than normal recruitment. Associated with the onshore transports were stronger than normal northward flows of the California Counter Current or Davidson Current. Southern fauna such as trigger fish and billfish were caught in late summer 1978 off California; possibly their presence there was in response to increased northward currents.

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In the Eastern Tropical Pacific, "anti-El Niño" conditions persisted throughout 1978 and early 1979, with strong upwelling and below normal sea-surface temperatures along the Equator. An index of the Southern Oscillation remained below normal, indicating generally weak trade winds and a low probability of El Niño conditions occurring in the near future.

in the Atlantic and Gulf coastal areas, 1978-79 was the third consecutive severely cold winter. These were the result of a deep and persistent atmospheric trough downstream from the west coast ridge. Three such cold winters in succession had never occurred before in the period of instrumental record in the United States. February air temperatures were lowest in 1978 south of Cape Hatteras on the Atlantic coast and in the northern Gulf of Mexico. In 1979 the greatest anomalies were found north of Norfolk, VA, on the Atlantic coast and in the northeastern Gulf of Mexico.

River runoff into Chesapeake Bay reached near or record high values in January and March in both 1978 and 1979, and also in May 1978. Flow into Long Island Sound reached record highs in January of both years, but remained near the long-term average values in other months. The Mississippi River flow reached relatively high, but not record, levels in March-May 1979, in contrast with the previous spring, when they were only about half as large.

Unusually large wind-driven transports occurred toward the south-southwest in December 1978 and toward the southwest in February 1979 in the southern New England area. These transports, the consequence of persistent west-northwest and northwest winds, occurred during the spawning periods of cod and haddock on Georges Bank. The drift of eggs and larvae in the plankton community in those months should have been strongly influenced by the anomalous transports. Off North Carolina there was a pronounced westward component in the wind-driven transport only in one month (February) of the 1979 winter spawning period of Atlantic menhaden. The component was less than half as large as that recorded in February 1978.

Sea-surface temperatures in the first three months of 1979 in the northwestern North Atlantic were up to 0.8°C (February) colder than the 1948-67 means for the area. The pattern was neither as intensive nor as extensive as that of January-March 1978. The pattern was similar in the Boothbay Harbor sea surface temperature data: anomalously cold in January-April 1979, but not as much as the comparable period in 1978. In the South Atlantic Bight, the anomaly pattern in the January-March periods of 1978 and 1979 were very similar, with February showing the largest negative anomalies, -1.24°C in 1978 and -1.36°C in 1979. Similar patterns were found in the Gulf of Mexico, once again showing the early months of 1978 to be colder than in 1979.

Apparently related to the variations in circulation and water masses was an absence of Gulf Stream warm core eddies near the continental shelf edge in the Georges Bank area during January-March 1978 and 1979. During these periods the Shelf Water/Slope Water front moved far seaward (up to 150 km) of its usual position near the edge of the Continental Shelf. The hiatus in eddy activity in 1978 was followed by an 8-month period (April-November) during which there was always an eddy or two adjacent to the bank, involving a total of six eddies. This period of eddy activity included the peak spawning months for several commercial species on the bank, but the amounts of eggs and larvae lost from the bank are unknown.

Bottom water on the shelf off southern New England (71°W) reached about the same minimum temperatures (<2°C) in February-March of both years, 1978 and 1979. In 1978 the unusually cold temperatures persisted in the mid-shelf cold cell into the summer period, remaining 1°-2°C lower than those measured during the previous four years. The offshore extension of the Shelf Water/Slope Water front was manifested in the bottom water also, reaching bottom depths of about 150 m in 1978 and 1979.

Off New Jersey the minimum bottom water temperatures in early 1978 were about 2°C warmer than 1977, but still were about 3°C colder than normal. By June, however, the cold cell bottom temperatures had warmed to about 4°C, about the same as in June 1977. In February 1979 bottom water temperatures were much like the minimum values of 1978, about 2°C in shallower water, but warmed 2°-4°C during the unusually mild March weather in the area. Seaward excursions of the Shelf Water/Slope Water front occurred in February-July and December 1978 and in March 1979. There was an absence of Gulf Stream warm core eddies off the middle Atlantic shelf during March-June 1978 and January-March 1979.

The Eastern Gulf Loop Current underwent a major northward extension (to about 30°N) into the Gulf of Mexico in spring and early summer of 1978. The timing of the extension fit the average pattern of variation, but the magnitude exceeded the average by about 3° latitude. The extension of Loop Current water onto the shelf is believed to have impacted on fisheries, yielding poorer harvests of brown shrimp, better catches of menhaden, and a red-tide bloom off the west Florida coast.

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RESULTS OF CIGUATERA ANALYSIS OF FISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Ciguatera is a form of fish poisoning caused by ingestion of certain species of fish. This study deals with the distribution of ciguatoxic fishes in waters of the Northwestern Hawaiian Islands (NWHI) and with a market sampling program to detect and remove ciguatoxic amberjack or kahala, Seriola dumerili, prior to its sale to the public. The results showed that ciguatoxic fish occurred throughout the entire NWHI from Nihoa to Kure Island. There were no detectable trends in rejection rate of the NWHI fishes with respect to area of capture; however, the analysis of data collected on kahala indicated a higher incidence of toxic fishes in the Nihoa-Raita Bank region. Of the 47 NWHI species tested between 1977 and 1979, the rate of rejection, based on a recently developed radioimmunoassay, was higher among fishes in the snapper-grouper complex. These included Caranx ignobilis, C. cheilio, Seriola dumerili, Epinephelus quernus, Etelis carbunculus, Lutjanus kasmira, and Pristipomoides filamentosus. Among inshore species sampled by the National Marine Fisheries Service and the Hawaii Division of Fish and Game, particularly high in rejection was Kuhlia sandvicensis and Cheilinus rhodochrous, followed by Myripristis amaenus, M. murdjan, Mugil cephalus, Caranx melampygus, Polydactylus sexfilis, and C. ignobilis. Of 926 kahala sampled between April and December 1979, 116 fish or 13% were rejected. The rate of rejection, high in April-May, declined steadily to December. The results also showed a low positive but significant correlation between fish size and toxicity.

Northwestern Hawaiian Islands
ciguatera
amberjack
snapper-grouper complex

INTRODUCTION

Ciguatera, a disease with certain characteristic neurotoxic and gastroenteritic symptoms produced by ingestion of a wide variety of fish belonging to groups such as the snappers, groupers, jacks, barracudas, surgeonfishes, and wrasses from toxic areas, appears to be widespread throughout the oceanic islands of the Pacific between the 30° parallels of latitude (Helfrich et al., 1968). The occurrence of ciguatera in some valuable food species found in the central Pacific affects not only the population by causing illness but also, as is often the case, deprives them of a major source of much needed protein. In areas that are seriously affected, it has restricted full development of fisheries and utilization of the available fish stocks.

At the outset of the Northwestern Hawaiian Islands (NWHI) survey and assessment investigation, provisions were made to conduct sampling for ciguatoxic fishes based on documented outbreaks of ciguatera occurring not only among the civilian population in the major Hawaiian Islands but also among U.S. naval and civilian personnel stationed at Midway Islands. It occurred to us that ciguatoxic fishes may also be found elsewhere in the archipelago and that the successful marketing of fishes caught in the NWHI would depend to a large extent on the wholesomeness of fishes from this area.

Together with the Hawaii Division of Fish and Game (HDFG), the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), initiated an extensive sampling program to study the occurrence and distribution of ciguatoxic fishes in the nearshore and offshore waters of the NWHI.

In the spring of 1979, following a sudden outbreak of ciguatera among the local populace, the Honolulu laboratory, together with other state agencies and the fishing industry, also began a project of routinely sampling and pretesting amberjack or kahala, Seriola dumerili, which had been implicated in most of the outbreaks. By mid-April 1979, information supplied by various governmental agencies and fish retailers indicated that about 30 to 35 recent outbreaks could be documented and that perhaps another 50 to 100 individuals were affected but had not reported it to the health authorities.

Prior to 1977, ciguatera research throughout the Pacific relied on relatively crude bioassays to detect the presence of toxin in fish tissues (Banner et al., 1960, 1961). It was not until 1977, when two significant breakthroughs were announced, did researchers see any way to solve some of the pressing problems dealing with ciguatera. One was the discovery of a dinoflagellate, originally misidentified as Diplopsalis sp., but subsequently identified as a new species, Gambierdiscus toxicus, as the likely causative agent in ciguatera outbreaks (Yasumoto et al., 1977) and the other was the development of the radioimmunoassay (RIA) method of detecting ciguatoxin by scientists at the University of Hawaii John A. Burns School of Medicine, Department of Pathology (Hokama et al., 1977).

METHODS

Initially, our sampling effort was concentrated on commercially important species; however, if time and circumstances permitted, we also sampled other less valuable species. From each fish, we obtained tissue samples from the dorsal musculature (A), ventral abdominal musculature (B), gonads (C), and liver (D). Subsequently, liver collection was discontinued and additional muscle tissue were collected from the anal region (E).

At sea as well as at the United Fishing Agency auction market where only kahala are sampled, each tissue collected is placed in a plastic vial, labeled, and either frozen (while at sea) or kept in the fresh state until processed. Data collected on the fish include date, catch location, water depth, sex, length, weight, and vessel name. When it was not possible to obtain exact catch locality, particularly for many of the kahala sampled at the fish auction market, broad geographical areas were substituted. Obtaining data on catch locality for the kahala is very difficult or impossible in some cases because fishermen who land their catches to be auctioned may have fished several islands and banks during the course of a trip and cannot provide exact information on where a particular fish was caught.

The samples are processed by the University of Hawaii Department of Pathology to determine toxicity levels of the fish tissues from radioactive counts per minute per gram of tissue (c/m/g). Based on studies of fish involved in clinically evaluated cases of ciguatera, and on mouse and mongoose toxicity tests, levels of toxicity were established as follows (Y. Hokama, University of Hawaii, John A. Burns School of Medicine, Pathology Department, Honolulu, personal communication):

c/m/g tissue	Toxicity levels
<350,000	Negative
350,000 to 399,999	Borderline
>399,999	Positive

RESULTS

About 16% of all the fish sampled by NMFS and HDFG showed either a positive or borderline rejection level when tested by the RIA method. Of the 1,494 fish sampled, 1,250 were negative, 148 were borderline, and 96 were positive.

Table 1 shows the results of the RIA for fishes sampled by the HDFG in the nearshore areas of the NWHI. Because the list of species sampled is lengthy (624 fish; 60 species) and many of the species had few samples, the table includes only those species for which 10 or more samples were available for the 3 years--1977 through 1979--combined. Among the species tested, Cheilinus rhodochrous had a rejection rate of 71% which is exceptionally high. This was followed by Myripristis amaenus with 45%, M. murdjan and Mugil cephalus, both with 18%, Caranx melampygus with 14%, and Polydactylus sexfilis and C. ignobilis, both with 13%. All of these are commercially valuable on the Hawaiian fresh fish market.

TABLE 1. THE NUMBER OF NEGATIVE (n), BORDERLINE (b), AND POSITIVE (p) REACTIONS (n-b-p) OBTAINED WITH THE RADIOIMMUNOASSAY CONDUCTED ON FISHES CAUGHT DURING NEARSHORE SURVEYS CONDUCTED BY HAWAII DIVISION OF FISH AND GAME. ONLY SPECIES WHERE 10 OR MORE SAMPLES WERE COLLECTED IN 1977-79 ARE INCLUDED.[1]

Species	1977	1978	1979	Rejection (%)
Carcharhinus menisorrah	--	8-0-0	3-0-0	0
Myripristis murdjan	--	5-2-0	4-0-0	18
M. amaenus	--	4-3-1	2-1-0	45
Polydactylus sexfilis	--	7-0-1	27-3-1	13
Kuhlia sandvicensis	--	2-1-2	47-2-0	9
Caranx ignobilis	24-5-2	16-3-1	47-2-0	13
C. melampygus	--	3-0-2	9-0-0	14
Mulloidichthys flavolineatus	--	1-0-1	31-1-1	9
Kyphosus cinerescens	--	2-1-0	11-0-0	7
Mugil cephalus	--	4-3-1	19-1-0	18
Bodianus bilunulatus	--	3-0-5	53-1-0	10
Cheilinus rhodochrous	2-2-10	2-0-0	1-0-0	71
Thalassoma duperreyi	--	0-1-1	53-1-0	5
Acanthurus triostegus	--	0-2-0	52-0-0	4

[1] Data from Henry Okamoto, Aquatic Biologist, Hawaii Division of Fish and Game.

Whereas the HDFG concentrated their sampling effort on nearshore fishes, the NMFS sampling included many of the offshore species, although some inshore species were included as a result of recreational fishing conducted during the Cromwell's refueling and rest stops at Midway (870 fish; 47 species). From Table 2, it can be seen that among the members of the carangids where 10 or more samples were collected, Caranx ignobilis had the highest rate of rejection, reaching 32% from 19 fish sampled. This was followed by C. cheilio with 11% rejection and Seriola dumerili with 10%. The only species of serranid, Epinephelus quernus, sampled during our survey had a relatively high rejection rate of 18%. Among the snappers, 3 of the 10 Etelis carbunculus or 33% showed hazardous levels of ciguatoxin followed by a 23% rejection rate among Lutjanus kasmira. Pristipomoides filamentosus also showed a relatively high rate of rejection, reaching 15% in our samples. Table 2 shows that most of the rejected fish were sampled at Necker and French Frigate Shoals.

Among the inshore fishes caught and sampled, only Kuhlia sandvicensis showed alarmingly high levels of ciguatoxin. Of the 47 fish sampled, 27, or 57%, were positive or borderline according to the RIA. This rate of rejection is considerably higher than that obtained from the HDFG nearshore samples collected from 1977 through 1979.

Most of the other fishes sampled were few in total numbers; therefore, it is difficult to draw definite conclusions about whether ciguatoxin occurs in any significant amounts in their tissues. None showed

TABLE 2. THE NUMBER OF NEGATIVE (n), BORDERLINE (b), AND POSITIVE (p) REACTIONS (n-b-p) OBTAINED WITH THE RADIOIMMUNOASSAY CONDUCTED ON FISHES CAUGHT DURING THE NATIONAL MARINE FISHERIES SERVICE SURVEY CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS IN 1977-79

	Nihoa	Necker	French Frigate Shoals	Brooks Banks	Gardner Pinnacles	Raita Bank	Maro Reef	Laysan	Northampton Seamount	Pioneer Bank	Neva Shoals	Lisianski	Unidentified Bank #8[1]	Pearl and Hermes	Midway	Kure	Unidentified Bank #10[2]	Total All Banks	Rejection (%)
Carangidae																			
Carangoides ferdau	--	--	--	--	1-1-0	--	--	--	--	--	--	--	--	1-0-0	--	--	--	2-1-0	33
Caranx cheilio	9-1-0	10-0-0	9-2-0	--	5-0-0	3-0-0	12-1-1	20-1-1	--	--	--	2-0-0	--	9-1-0	4-1-0	8-1-1	--	91-8-3	11
C. ignobilis	--	--	5-1-1	--	2-0-0	--	--	2-0-0	--	3-3-1	--	--	1-0-0	--	--	--	--	13-4-2	32
C. lugubris	--	--	--	--	1-1-3	--	--	--	--	--	--	--	--	--	--	--	--	1-1-3	30
C. melampygus	--	1-0-0	--	--	2-1-0	--	--	--	--	--	--	--	--	--	--	--	--	3-1-0	25
C. speciosus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	11-0-0	--	--	11-0-0	0
Elagatis bipinnulatus	--	2-0-0	--	--	1-0-0	--	--	--	0-1-0	--	--	--	--	--	--	--	--	3-1-0	25
Seriola dumerili	2-0-1	15-0-3	5-1-0	2-0-0	2-0-0	2-0-0	8-0-1	12-1-1	--	--	2-0-0	6-0-0	5-0-0	19-0-0	2-0-1	1-0-0	--	83-2-7	10
Serranidae																			
Epinephelus quernus	2-1-0	6-0-0	11-1-0	0-0-3	4-3-1	3-0-0	16-2-5	4-0-0	4-0-0	3-0-2	6-0-0	7-0-0	7-1-1	18-0-0	--	7-2-0	2-0-0	100-10-12	18
Lutjanidae																			
Aprion virescens	1-1-0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1-1-0	50
Etelis carbunculus	--	--	--	--	--	--	--	2-0-0	--	--	--	--	--	2-0-1	--	3-2-0	--	7-2-1	30
E. marshi	--	--	2-0-0	--	4-0-0	--	15-0-0	8-1-0	4-0-0	--	7-0-0	--	8-1-0	17-3-0	--	--	--	65-5-0	7
Lutjanus kasmira	11-1-3	1-0-0	11-2-2	4-0-0	--	--	--	--	--	--	--	--	--	--	--	--	--	27-3-3	23
Pristipomoides filamentosus	4-0-0	51-6-3	27-10-1	--	7-0-0	--	17-1-0	17-1-0	6-0-0	1-0-0	2-0-0	1-0-0	--	0-1-0	--	--	--	133-19-4	15
P. sieboldii	--	4-0-0	2-0-0	1-0-0	--	1-0-0	1-0-0	--	1-0-0	--	--	--	--	3-1-0	--	--	--	13-1-0	7
P. zonatus	--	--	5-0-0	1-0-0	--	--	6-0-0	0-0-1	2-0-0	--	1-0-0	--	7-0-0	1-0-0	--	--	--	23-0-1	4
Kuhliidae																			
Kuhlia sandvicensis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	20-12-15	--	--	20-12-15	57

[1] Unidentified bank #8 is located at lat. 26°17'N, long. 174°34'W.

[2] Unidentified bank #10 is located at lat. 28°58'N, long. 178°42'W.

exceptionally high rejection rates, although mention should be made of some members of the families Muraenidae and Acanthuridae that showed presence of ciguatoxin in varying degrees. These would include *Gymnothorax flavimarginatus*, *G. hepaticus*, *Acanthurus triostegus*, and *A. nigroris*.

In the kahala testing program, which began in April 1979, the number of fish tested until the end of December 1979 reached 926. Of these, 78 were borderline and 38 were positive in the RIA for a total rejection of 116 fish, or 13%. The rejection rate was relatively high in April 1979 when 63% of the kahala sampled were rejected but decreased in May to 24%, in June to 16%, then fluctuated between 3 and 6% until December when the rejection rate rose slightly to 10% (Table 3).

TABLE 3. THE NUMBER OF KAHALA SAMPLED WITH RIA, BY MONTH, THE NUMBER AND PERCENTAGE OF NEGATIVE, BORDERLINE, AND POSITIVE REACTIONS OBTAINED WITH THE RIA, AND THE TOTAL NUMBER AND PERCENTAGE OF FISH REJECTED PRIOR TO SALE

1979	Total Sampled	Negative	%	Borderline	%	Positive	%	Total Toxic	%
Apr.	52	19	37	10	19	23	44	33	63
May	122	93	76	21	17	8	7	29	24
June	174	147	84	24	14	3	2	27	16
July	153	149	97	4	3	0	0	4	3
Aug.	92	88	96	4	4	0	0	4	4
Sept.	73	71	97	2	3	0	0	2	3
Oct.	90	87	97	3	3	0	0	3	3
Nov.	65	61	94	1	1	3	5	4	6
Dec.	105	95	90	9	9	1	1	10	10
Total	926	810		78		38		116	

According to information provided by the fishing vessels, the area of capture of these kahala varied from as far south as the island of Hawaii northwestward to Raita Bank, a distance that spans 1,723 km. By geographical area, then, it appears that rejection was higher among kahala caught in the NWHI, principally from the area between Necker and Raita Bank, with the rejection level reaching 32% (Table 4). This was followed by a rejection rate of 29% among fish caught off the south coast of Oahu, and a rate of 24% among fish caught off Maui. Fishes caught at Penguin Bank also were rejected at a fairly high rate of 17%

Of particular interest is the relationship between fish size and toxicity. Prior to the start of the kahala sampling program, sale of fish weighing 9 kg (20 lb) or more was usually discouraged, because ciguatera outbreaks in the past allegedly implicated fish that were 9 kg or more in weight. Examination of our data showed that the size of kahala sampled between April and December 1979 varied from 0.57 to 45.4 kg (1.25 to 100.25 lb). Fish that were rejected fell in a range

TABLE 4. THE NUMBER OF KAHALA SAMPLED BY AREA AND THE NUMBER AND PERCENTAGE REJECTED BASED ON RESULTS OF RADIOIMMUNOASSAY

Area of Capture	Number Sampled	Number Rejected	% Rejected
Gardner Pinnacles	153	10	6
Necker-Raita Bank	132	42	32
Nihoa	1	0	0
Kauai	1	0	0
Oahu			
Southeast Coast	34	3	8
South Coast	77	22	29
North Coast	32	4	12
Molokai	5	0	0
Penguin Bank	151	26	17
Maui	17	4	24
Hawaii			
East Coast	192	12	6
South Coast	12	0	0
Unknown	119	9	7

from 0.79 to 26.88 kg (1.75 to 59.25 lb). Preliminary analysis showed that there is a low positive but significant correlation between toxicity level (tissue E) and fish size ($r = 0.101$; df = 1,202; $p < 0.01$).

DISCUSSION AND CONCLUSIONS

The preliminary results obtained from our NWHI samples show some agreement with those given by Sylvester et al. (1977). In the snapper-grouper complex of fishes in the Virgin Islands (includes snappers, groupers, grunts, jacks, porgies, triggerfishes, filefishes, and wrasses), the family Carangidae contains the most species prone to be ciguatoxic, followed by snappers and groupers. All are carnivores that attain relatively large sizes.

It is interesting to note that Pristipomoides filamentosus, considered to be a top-quality food fish and highly prized on the local fresh fish market, had a rejection rate of 15%. Yet, this species has never been implicated in any outbreaks among local citizens (Kubota, 1972).

According to Hokama et al. (1977), the RIA may produce "false positives." The binding of the anti-ciguatoxin-human serum albumin to non-toxic fish could be due to sensitivity of the test, to cross-reacting antigenic determinants, or to non-specific binding. There is also the possibility that most, if not all, marine fishes already contain low undetectable levels of ciguatera-like compounds. It should be emphasized, however, that although some "false positives" may occur as a result of the binding of anti-ciguatoxin-human serum albumin to non-toxic fish tissues, this should not detract from the value of the test. As demonstrated by Hokama et al. (1977), clinically documented toxic fishes

(fishes that have been actually implicated in ciguatera outbreaks) have given significantly higher c/m/g tissue than non-toxic fishes.

FUTURE RESEARCH NEEDS

Although NMFS field sampling included 47 species, most of which came from our offshore stations, it appears now that effort will need to be redirected to gather more data and samples from members of the families belonging to the snapper-grouper complex, all of which are commercially valuable in the Hawaiian Islands. With few exceptions, members of this complex showed varying rates of rejection with the RIA.

Processing of biological samples will continue so that the data base may be strengthened with respect to diet and sexual maturity and relationships of these variables to toxicity may be examined. Additional areal and seasonal coverage is also needed so that the distribution and seasonal occurrence of ciguatoxic fishes can be more clearly understood. Also planned are in-depth statistical analysis of the data collected from the NWHI fishes and of the data collected in the kahala testing program.

SUMMARY

From 1977 through 1979, NMFS and HDFG sampled 1,494 fish in the nearshore and offshore waters of the NWHI for ciguatera analysis. Of these, 244, or 16%, were rejected because the detected levels of ciguatoxin with RIA were considered hazardous to humans. Ciguatoxic fishes occurred throughout the NWHI and no apparent trend could be seen in their distribution. In the kahala sampling program, the data indicated a higher rate of rejection among fish caught between Nihoa and Raita Bank than among those caught in waters around the major islands. Of 926 kahala sampled between April and December 1979, 116 fish or 13% were rejected. Preliminary analysis suggests that there exists a low but statistically significant positive correlation between kahala size and toxicity.

Among the offshore species sampled by NMFS, those that belong to the snapper-grouper complex showed a relatively high degree of rejection. Nearshore species that showed high rejection rates included *Kuhlia sandvicensis* and *Cheilinus rhodochrous*.

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Tracking Pelagic Dolphins by Satellite

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Abstract — A satellite-linked tracking system is being designed for assessing numbers of dolphins involved in the yellowfin tuna fishery of the eastern tropical Pacific, U.S.A. Testing is via the NIMBUS-6 satellite. The transmitter has a 17.8 cm one-quarter wavelength stub antenna, operates at 401.2 MHz, has a power output of 0.5 W, and incorporates a seawater switch to regulate transmission. Preliminary tests in the laboratory and on captive dolphins revealed problems with the bit rate oscillator, the seawater switch, and frequency modulation. Field tests of prototype transmitters on wild Hawaiian spotted dolphins are scheduled for spring, 1979.

INTRODUCTION

Under the U.S. Marine Mammal Protection Act of 1972, the National Marine Fisheries Service (NMFS) was made responsible for conservation of dolphins involved in the yellowfin tuna fishery of the eastern tropical Pacific, U.S.A. Regulations governing the fishery, including dolphin mortality quotas, are based on determinations of the status of the stocks. Assessment of animal populations requires data on distribution, migration, and mixing of the stocks, as well as on numbers. These data are combined with age, sex, and growth information obtained from sampling the kill to determine the status of the stocks.

The area involved in the fishery is substantial — 13 million km^2. NMFS conducts aerial surveys, but the range of the relatively low flying planes limits coverage. A conventional tagging study is planned using highly visible disc tags placed on the dorsal fin. Cost of the tags is minimal, but charter cost for a tuna purse seiner (which is the only means of catching large schools of dolphins) is approximately $10,000 per day. Tagging studies generally provide data at only two locations — the site of tagging and that of recovery. Radio tracking using standard HF and VHF equipment generally involves tracking one animal for a limited time and there is always the risk of losing the animal.

PRELIMINARY TESTS

Initial development of the system concentrated on antenna selection. A 17.8 cm one-quarter wavelength stainless steel stub was chosen. Preliminary tests on a captive dolphin were conducted at Sea World, San Diego, California, in June, 1977, using a modified engineering model of a satellite-linked transmitter developed for use on buoys. These tests, as well as all other work to date, have used the Random Access Measurement System (RAMS) on the NIMBUS-6 satellite. The purpose of the test was to assess the impedance match of the antenna, transmitter, and a live dolphin. The animal was trained to surface on command for transmission every 64 s. A minimum of four successful up-links (transmission to the satellite) per satellite orbit is required to accurately determine position. Of the 14 tests conducted from the live dolphin, only 2 tests were successful with the satellite receiving 4 and 5 up-links. Of 23 verification tests conducted with the transmitter on a roof, 10 were successful with as many as 15 up-links. Failure to achieve sufficient up-links was attributed to several factors: the satellite recorders were sometimes turned off; high satellite elevation angles may have occasionally been a problem; a defective battery cell caused the voltage to drop off after 36 h when it was designed to last 72 h; and the oscillator was not adequately temperature compensated. Most importantly, it was later discovered that the RF oscillator did not fully stabilize until 15 min after power was supplied. Since we did not turn on the unit until immediately before the satellite pass, the frequency drift was too great for reception by the satellite receiver. The test did successfully demonstrate that the concept is feasible and that geographic position of the platform could be determined (Gandy, Vanselous and Jennings, 1977).

MATERIALS AND METHODS

A new prototype transmitter pack is being designed and built. The engineering model consisted of: a power supply of 18 3-VDC organic lithium cells; main timing circuit; RF oscillator and power amplifier; seawater activation switch; one-quarter wavelength stub antenna; and aluminum (6061) housing. The system is currently packaged in two cylindrical tubes each measuring 17.5 × 5 cm, which are connected by a 1.61 cm diameter neoprene tube. The pack weighs 907 g. The system operates at a frequency of 401.2 MHz with a transmission repetition rate controlled by the seawater switch. The transmission rate is one message per second if the switch circuitry is inhibited.

Laboratory tests were conducted in November, 1978 and February, 1979, using a RAMS satellite simulator, to evaluate the transmitter's operating characteristics such as frequency variation, phase modulation, proper message formating and transmission timing.

Field tests on dolphins were conducted during 8-14 February, 1979, at Sea Life Park, Hawaii, using the engineering model. The package was attached with a nylon harness to the area of the dorsal fin of a captive dolphin. A receiver was located near the habitat pool, so that the operational status of the transmitter could be monitored. Satellite data were obtained by telephone through the NIMBUS Control Center at NASA's Goddard Space Flight Center, Greenbelt, Maryland, U.S.A. A test schedule was established, based on predicted times of overpasses and elevation angles of the satellite. Angles greater than 23^{o} were chosen in order to have maximum time during the passes. The duration of these passes was about 20 min.

RESULTS

The engineering model failed the initial laboratory test in November, 1978 due to excessive frequency drift and improper phase modulation. The unit successfully interrogated the simulator during the second laboratory test in February. However, three problem areas were identified: (1) the frequency variation was 1.5 Hz min^{-1} versus a design specification of 0.28 Hz min^{-1}; (2) the four data channels of the simulator received random messages; and (3) the seawater switch tended to lock in the 'on' position causing the transmitter to operate at the maximum repetition rate of one message per second.

Eight tests of the engineering model were conducted on a captive dolphin. Sufficient up-links to determine geographic position were achieved during five overpasses (Table 1). The average error in calculated position was 23.33 km, reflecting frequency instability in the transmitter and possibly a larger longitudinal computation error at higher satellite elevation angles. The loss of data for two overpasses was due to the failure of the seawater switch in one case and the spacecraft recorder not being turned on in the other. The third failure is unexplained.

Table 1.
Reported position of transmitter
(Actual location was 21.32°N-157.66° W)

Date (calendar)	Time (GMT)	Reported position (Latitude)	Reported position (Longitude)	Computed error (km)
2-11-79	2212	21.32°N	158.07°N	44.4
2-12-79	0934	21.14°N	157.46°W	29.6
2-12-79	2125	21.35°N	157.63°W	9.3
2-14-79	0941	21.34°N	157.96°W	33.3
2-14-79	2149	21.32°N	157.66°W	0

CONCLUSION

Tests have shown that it is feasible to acquire data on geographic positions of marine animals with a satellite-linked tracking system. Four design changes were implemented in recent tests: (1) RF shielding of the seawater switch circuit; (2) an inhibit circuit to prevent the transmitter from operating continuously when the animal is at the surface; (3) temperature compensation of the bit rate oscillator; and (4) frequency stability to within 0.28 Hz min^{-1}.

Two prototype units with these modifications will be tested on wild Hawaiian spotted dolphins (*Stenella attenuata*) in offshore Hawaiian waters in the spring of 1979. Successful tracking of these dolphins is prerequisite to placing transmitters on wild dolphins of the same species in the fishery. Placement on wild dolphins in the eastern tropical Pacific could begin in late 1979. Transition to the TIROS-N satellite is being evaluated which would require some modification of the electronics.

The tracking system is being designed to be applicable to other marine animals such as large whales and sea turtles. The pack will be reduced in size, and could be designed to incorporate oceanographic and physiological sensors.

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PRELIMINARY STUDY ON THE SPAWNING SEASON OF THE OPAKAPAKA, *PRISTIPOMOIDES FILAMENTOSUS*

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ABSTRACT

As part of the survey and assessment program of the Northwestern Hawaiian Islands, the National Marine Fisheries Service has been studying the distribution, apparent abundance, and biology of commercially valuable bottomfish. This study deals with the reproductive cycle of the opakapaka, *Pristipomoides filamentosus*, one of the most important snappers in the Hawaiian fishery. The results showed that the development of ova within the paired ovaries is heterogeneous. Stages of maturation, determined from the development of ova in the most advanced mode in the distribution of random ova diameters, showed a positive relationship with the gonadal somatic indices. The gonadal somatic index peaked in August with spawning possibly taking place in September.

opakapaka
reproduction
Northwestern Hawaiian Islands

INTRODUCTION

The opakapaka or pink snapper, *Pristipomoides filamentosus* Cuvier and Valenciennes, which has been fished intensively around the Hawaiian Archipelago for decades, is the most important bottomfish in terms of landed weight and cash value. This snapper is prized for its good taste and pleasing appearance (Brooks Takenaka, Assistant Manager, United Fishing Agency, Honolulu, Hawaii, personal communication, January 1980).

There is a limited amount of literature on the life history and biology of the opakapaka. Most papers written about the opakapaka deal with the fishery.

In 1976, the National Marine Fisheries Service (NMFS), Honolulu Laboratory initiated a resource assessment program for the Northwestern Hawaiian Islands (NWHI). Part of the program deals with the bottomfish resource and its interaction with the ecosystem. This study examines the spawning behavior of the opakapaka.

METHODS

For a major part of the resource assessment program, the NOAA ship Townsend Cromwell was used to survey the bottomfish resource in the NWHI. The opakapaka with other bottomfishes were caught on handline gear using four hooks (No. 26) per line. The lines were retrieved by four powered gurdies on the starboard rail. Opakapaka were usually caught between 40 and 120 fathoms.

The fish landed were measured for fork length (FL) and standard length (SL) in millimeters and weighed to the nearest 10 g. Otoliths, gonads, and stomach content samples were removed and retained for further studies. Samples were preserved in 4% formaldehyde and seawater. No quantitative observations were taken on the preserved ovarian material until 6 or more months had passed and shrinkage had been stabilized.

Homogeneity

A pair of ovaries was examined for homogeneous development of the ova. A No. 5 cork borer with an inside diameter of 10.026 mm was used to extract core samples from the anterior, middle, and posterior regions of both ovaries. Each of the core extended from the outer surface of the ovary to the centrally located lumen and was divided into an outer layer, central layer located adjacent to the lumen, and a middle layer, thus providing a total of 18 subsamples. Developing ova were teased from each of the 18 subsamples and 200 randomly selected ova were measured.

Spawning seasonality

For the spawning season of the opakapaka, 21 ovaries collected between February 1978 and June 1979 were examined. Maturity of the ovary was determined by examining the middle core sample. Four hundred randomly selected ova were classified according to stage of maturity from the three layers of the cored sample. The mean of the last two advanced modes were taken to determine ovarian maturation state.

Developmental stages of the ova

The developmental stages, determined on the basis of physical appearance (Uchiyama and Shomura, 1974), are described as follows:

1) Primordial

Primordial ova are found in all the ovaries, usually ovoid in structure and transparent. No ova diameters were measured.

2) Early developing ova

Ova are transparent to translucent with the beginning of opaque yolklike matter in the ovum. The shape of the ova is usually ovoid or wedgelike. Size range: 0.15 to 0.39 mm in diameter.

3) Developing ova

Ova are completely opaque and ovoid. Size range: 0.16 to 0.67 mm in diameter.

4) Advanced developing

Ova are ovoid and have a translucent margin. The fertilization membrane has formed. Size range: 0.39 to 0.60 mm in diameter.

5) Early ripe

Ova are usually round or spherical. The yolk material is translucent and the oil globules have formed. Size range: 0.47 to 0.58 mm in diameter.

6) Ripe ova

Ova are transparent and contain oil globules. No ovary in the ripe condition was collected.

7) Residual ova

Ova are degenerating and show signs of shrinking.

RESULTS

Homogeneity of development

In the test of homogeneity, ovary No. 14 was selected and the ova diameters in the developing stage from each of the 18 sites were compared. The frequency distributions of the diameters were skewed to the right of the mean. A Kruskal-Wallis non-parametric test (Sokal and Rohlf, 1969) was used to test the homogeneity of locations for the distributions of ova diameters for the 18 sites. The results showed that the locations of the 18 distributions differed significantly ($X^2 = 191.45$, df = 17, $P = 0.05$). The development of the ovary in the opakapaka is therefore heterogeneous. Heterogeneous development of large ovaries were also demonstrated in the bigeye tuna, *Thunnus obesus*, by Yuen (1955), in the albacore, *T. alalunga* by Otsu and Uchida (1959), and in the swordfish, *Xiphias gladius*, by Uchiyama and Shomura (1974).

Spawning season

The gonadal somatic index (GSI), because it can be easily calculated, can be used to reduce time-consuming and tedious examination and measurement of the ova, provided it can be shown to have a positive relationship with stages of maturity (Table 1). To explore this possibility, a test was conducted initially to determine whether fish size was related to the GSI; however, no significant correlation was obtained ($r = 0.025$; df = 20; $P > 0.05$), indicating that fish size was not associated in any way to the GSI. A test between fish size and stages of maturity also showed no significant correlation ($r = 0.212$; df = 20; $P > 0.05$). When GSI was plotted against stages of maturity, however, there was an indication of a positive trend. A test of the relationship between GSI and stages of maturity showed a significant positive correlation ($r = 0.540$; df = 20; $P < 0.01$), but because only two samples past the early developing stage were available, the relationship cannot be accepted as conclusive (Figure 1). It would appear, however, that as females mature, the weight of the ovary not only increases faster than the total body weight, but also rises and falls in relation to development, spawning, and redevelopment.

To determine the spawning cycle of the opakapaka, GSI was plotted against the month of capture. The results show that it reached its lowest level in March and peaked in August (Figure 2). The opakapaka, therefore, appears to have one spawning period each year in early fall, probably in September (Table 1).

DISCUSSION

By examining conditions and occurrence of the early ripe and advanced developing ova throughout the 18 sites, it was possible to determine visually that development of the ovary in the opakapaka was heterogeneous. Of the total 18 subsamples from one fish, only six subsamples had ova in the advance developing stage and two subsamples had ova in the early ripe stage.

In the test for homogeneity of location, developing ova were used because of their consistency throughout the 19 subsamples.

TABLE 1. FORK LENGTHS, GONAD WEIGHTS, GONADAL SOMATIC INDICES, AND STAGES OF MATURATION OF 28 OPAKAPAKA SAMPLED BETWEEN FEBRUARY 1978 AND JUNE 1979

Sample No.	Date of Catch	Fork Length (cm)	Fish Weight (kg)	Preserved Gonad Weight (g)	Gonadal Somatic Index[1]	Maturity[2]
1	10/25/78	70.1	5.28	58.61	1.11	Dev.
2	8/09/78	60.4	3.72	--	--	Dev.
3	8/11/78	71.4	5.58	58.84	1.05	Dev.
4	10/25/78	72.7	5.05	37.16	0.74	Imma.
5	--	58.7	3.69	64.00	1.73	Adv. Dev.
6	8/09/78	66.2	4.66	--	--	Dev.
7	8/09/78	63.1	4.00	54.68	1.37	Dev.
8	9/13/78	62.1	4.00	96.22	2.41	Imma.
9	8/11/78	72.22	5.88			
10	9/13/78	52.0	2.52	89.44	3.55	Resid.
11	9/17/78	76.3	6.49	136.16	2.10	Adv. Dev.
12	9/17/78	48.7	2.02	33.61	1.66	Dev.
13	9/19/78	--	--	20.81	--	Dev.
14	8/24/78	67.1	5.45	223.42	4.10	Early Ripe
15	10/ /78	54.0	2.18	35.81	1.64	Adv. Dev.
16	10/ /78	52.0	2.49	36.38	1.46	Adv. Dev.
17	10/ /78	59.0	2.81	14.09	0.50	Adv. Dev.
18	10/ /78	58.0	2.36	--	--	Adv. Dev.
19	3/05/78	57.3	3.00	11.12	0.37	Imma.
20	3/05/78	55.4	2.90	10.99	0.38	Imma.
21	10/ /78	71.0	5.53	152.8	2.76	Adv. Dev.
22	3/06/78	73.5	6.30	40.85	0.65	Imma.
23	2/26/78	52.6	2.17	10.34	0.48	Imma.
24	3/06/78	64.0	5.40	25.57	0.47	Imma.
25	2/26/78	68.3	5.30	28.78	0.54	Imma.
26	6/02/79	45.6	2.10	38.01	2.10	Dev.
27	5/18/79	94.7	6.90	74.70	1.37	Dev.
28	5/23/79	74.9	--	--	--	Dev.

[1] Gonadal somatic index = $\frac{\text{gonad weight}}{\text{fish weight}} \times 100$

[2] Dev. = developing ova; Imma. = immature ova; Adv. Dev. = advanced developing ova; and Resid. = residual ova.

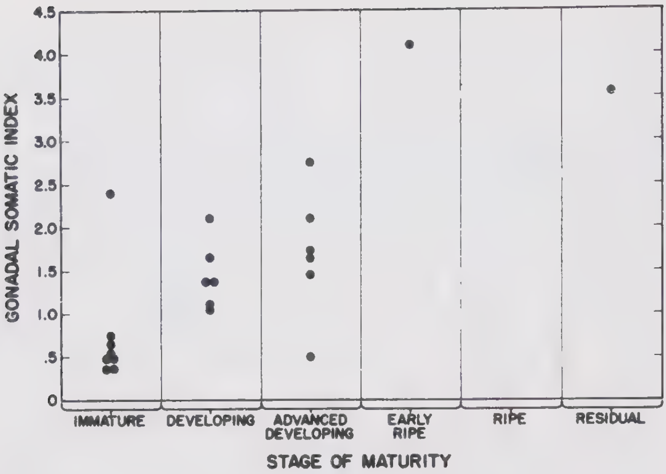

Figure 1. Relationship between stages of maturity and gonadal somatic index in the opakapaka, Pristipomoides filamentosus

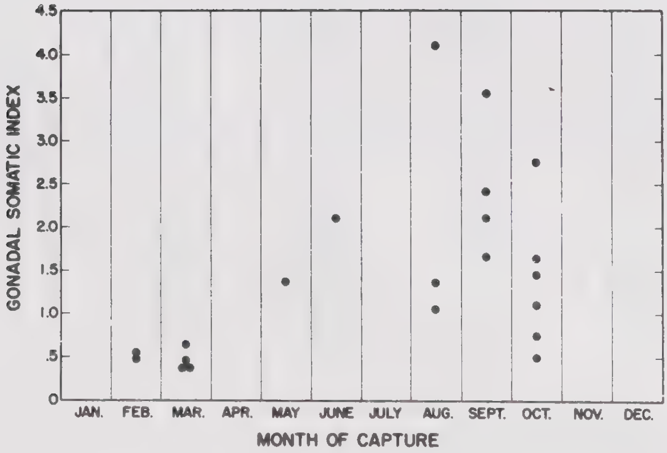

Figure 2. Relationship between month of capture and gonadal somatic index in the opakapaka, Pristipomoides filamentosus

FUTURE RESEARCH NEEDS

More opakapaka need to be sampled between November and July, including a wide range of gonads to determine minimum size of spawning and sexual maturity. It is important that ripe ovaries be obtained to better understand ovary development, fecundity, and spawning cycles.

SUMMARY

Preliminary results show that the opakapaka ovaries develop heterogeneously.

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Variability in Techniques of Counting Dentinal Growth Layer Groups in a Tooth of a Known-Age Dolphin, *Tursiops truncatus*

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ABSTRACT

A photograph of a mid-longitudinal tooth section of a known-age bottlenose dolphin was used to evaluate the techniques of six experienced tooth readers in counting the growth layer groups (GLGs).

The results point up the problem of using different criteria to define GLGs. When age is known, GLG counts may be similar even if somewhat different landmarks in the tissue are used. However, when age is unknown, GLG definitions tend to be more variable among readers using different criteria. The results of the present exercise suggest a critical need to intercalibrate the various aging techniques for given species.

INTRODUCTION

The method of age determination in odontocete or toothed whales according to the number of layers in the dentine was first developed for striped dolphins *(Stenella coeruleoalba)* by Nishiwaki and Yagi (1953). Subsequently it was applied to sperm whales *(Physeter macrocephalus)* by Nishiwaki, Hibiya and Ohsumi (1958); to white whales *(Delphinapterus leucas)*, pilot whales *(Globicephala melaena)*, and bottlenose dolphins *(Tursiops truncatus)* by Sergeant (1959); and to common dolphins *(Delphinus delphis)* by Kleinenberg and Klevezal′ (1962). In recent years, the method has become standard procedure for determining age in many other odontocetes.

In the course of dental appositional growth, layers of differential mineral and optical density are accumulated in the dentine in complex patterns. Although in many cases prominent 'annual' layers may be distinguished in sectioned teeth, two or more prominent sublayers (i.e. accessory layers) within each annual layer may be apparent also. The presence of accessory layers has made difficult the delineation of annual layers; they may be counted inadvertently as annual layers.

Berzin (1964) and Klevezal′ and Kleinenberg (1967) discussed the problems posed by the existence of accessory layers; the latter authors called attention to the need to calibrate dentinal layers because of the continuing disagreement among workers arising from differing interpretations of accessory layers. In 1968, the International Whaling Commission sponsored a special meeting of sperm whale biologists from several nations to resolve differences in tooth-reading methods and to agree upon a standard descriptive terminology (IWC, 1969). As a result of the meeting, the following terms were defined: *Lamina* – a translucent or opaque zone in the dentine. The *translucent zone* appears clear or light in transmitted light, dark in reflected light. The *opaque zone* appears dark in transmitted light, light in reflected light. A *growth layer* (layer) consists of two adjacent laminae, one translucent, the other opaque.

Sergeant (1959), Sergeant, Caldwell and Caldwell (1973) and Hui (1978), who independently undertook studies of teeth of a few known-age bottlenose dolphins in attempts to identify annual dental layers, obtained layer counts that correspond to the ages of the animals. In many cases however, the definition of countable layers (GLGs, terminology of the workshop report – this volume) continues to be highly judgmental and variable among workers. This may be due chiefly to the wide variety of criteria used in defining layers.

To examine this problem more thoroughly, an exercise was conducted that compared the methods of six experienced tooth readers in defining GLGs of a tooth of a bottlenose dolphin of known age. Since the true age of the animal represented was withheld from four of the six readers, one of the aims of the experiment was to compare various methods of GLG identification rather than to determine the accuracy of GLG counts in relation to age. Comparison of the interpretations between the two readers who had access to the age information was carried out to evaluate the criteria used in defining the GLGs when age is known.

MATERIALS AND METHODS

The material for the present exercise consisted of a photograph of a mid-longitudinal section of an acid-etched tooth from 'Pinger', a 3.3-year-old bottlenose dolphin, *Tursiops truncatus,* which was born on 4 November 1970 and died on 4 February 1974. The photograph was used in an earlier calibration study (Hui, 1978). Preparation of the section was described by Hui (ibid).

Copies of the photograph were distributed to six tooth readers experienced in aging delphinids. To facilitate comparisons of GLG definitions among the readers, the same part of the tooth section in each photograph was overlain with a strip of clear plastic tape. Each participant was instructed to record his readings of GLGs on the tape (Fig. 1).

RESULTS

The photograph of the thin-sectioned tooth (Fig. 1) shows three thick layers of postnatal dentine separated from each other by strongly optically opaque boundary layers. These thick layers contain two or more sublayers, each separated from the other by thin, optically opaque boundary layers of variable intensity.

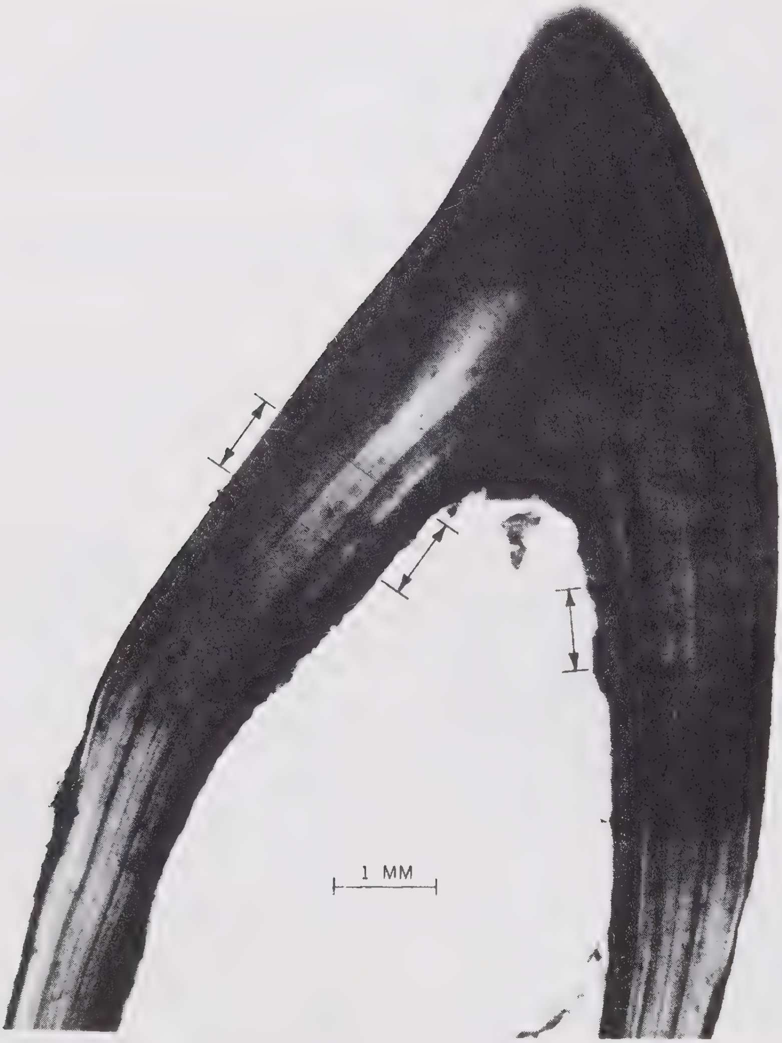

Fig. 1. Photomicrograph of longitudinal tooth section of the 3.3-year-old specimen of *Tursiops truncatus*.

The GLGs as defined by the six participants are compared in Fig. 2. The interpretations made by Coe, Perrin, Hui and Kimura are similar. Perrin, Coe and Kimura used the strongly opaque layers to divide the postnatal dentine tissue into three and a fraction GLGs, but Hui used a thin, translucent layer adjacent to each strongly opaque layer to separate GLGs. Sergeant used the primary (strongly opaque) and some of the more intense secondary (thin opaque) boundary layers to divide the tissue into six and a fraction GLGs. Miyazaki's interpretations were similar to those of Sergeant except for the third GLG defined by Miyazaki, in which Sergeant identified two GLGs. Miyazaki's count was five and a fraction GLGs.

DISCUSSION

Although GLG counts made by Coe, Perrin, Kimura and Hui corresponded closely, the criteria used by Kimura and Hui (to whom Pinger's age was known) differ from each other somewhat. Miyazaki's and Sergeant's GLG definitions were similar, but their counts differed from each other by one GLG and from those of the other participants by two and three GLGs, respectively.

The results of the exercise point up the problem of using different criteria to define GLGs. When age is known, as in the cases of Kimura and Hui, GLG counts may be similar using somewhat different landmarks in the tissue. However, when age is unknown, as in the cases of Coe, Perrin,

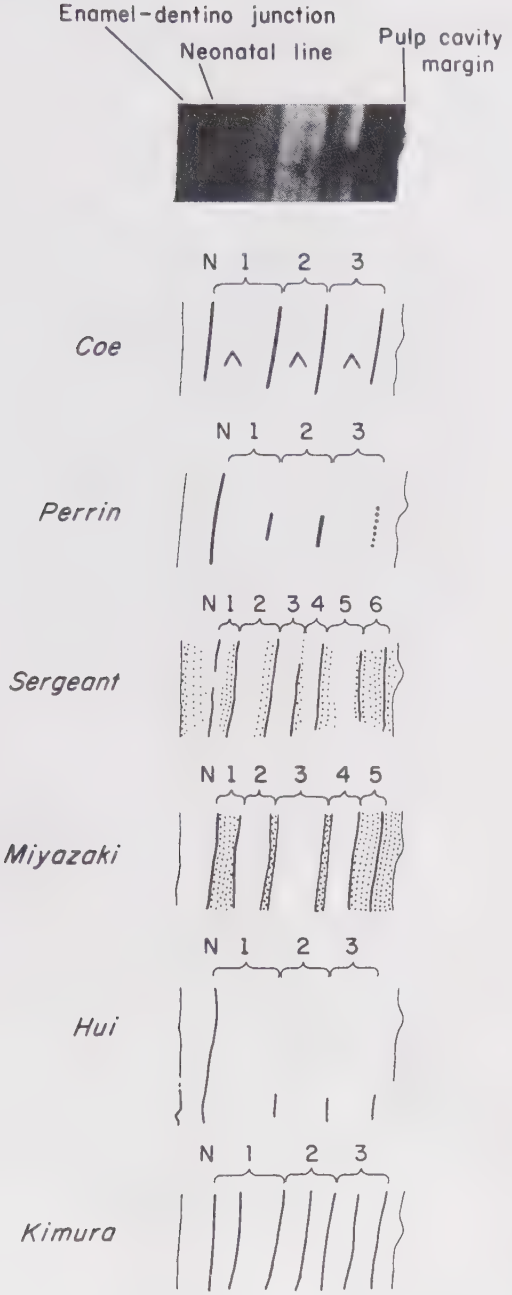

Fig. 2. GLG counts for the 3.3-year-old specimen of *Tursiops truncatus* as estimated by various readers. Inverted v's indicate accessory layers. The photograph of the field in the tooth section where the GLG counts were made is shown on the top.

Sergeant and Miyazaki, GLG definitions tend to be more variable among readers using different criteria.

Dentinal GLGs are complex in pattern and variable in optical density. Because of the wide range of preparation and counting techniques in use, there remains a critical need to intercalibrate the various techniques used for dental age determination for given species. Without precise definitions of what units are being counted, the existing confusion over growth rates, age composition, and other life history parameters of odontocete species will go unresolved.

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LASKER AND BROWN: FREE-FALL PARTICLE COUNTER FOR OCEAN SURVEYS
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FREE-FALL PARTICLE COUNTER FOR OCEAN SURVEYS

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ABSTRACT

For a study of particles in the sea as potential food organisms for larval anchovies (Lasker 1975, 1978), a survey method was needed to profile particle concentrations with depth rapidly during California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys.

To do this, a microprocessor-based free-fall particle counter (FFPC) was designed and constructed (Brown 1977) based on the well-known principle that a particle passing into an electrical field in an electrolyte causes a change in electrical properties if resistivity of the particle differs from that of the electrolyte. The widely used Coulter Counter® is an example of an instrument based on this principle.[1] In this report, laboratory calibration and a field test of the FFPC are described as well as modifications to the instrument that permit fast deployment of the probe, shipboard display, and printing of the data.

RESUMEN

Para un estudio de partículas en el mar como organismos potenciales de alimentación para larvas de anchoveta (Lasker 1975, 1978), se necesitaba un metodo rápido para poder perfilar concentraciones de partículas con la profundidad, durante los cruceros de reconocimiento de CalCOFI.

Para hacer ésto, un contador de partículas de caída libre basado en un microprocesador fue diseñado y construido, basado en un principio bien conocido de que una partícula, al pasar por un campo eléctrico en un electrolito, causa un cambio en las propiedades eléctricas si la resistividad de la partícula difiere de la del eléctrolito. Un ejemplo de un contador que está basado en este principio y que se usa mucho es el Coulter Counter®[1]. En este trabajo, se describe la calibración en el laboratorio y la prueba práctica del contador, así como modificaciones del instrumento que facilitan el despliegue rápido de la sonda, una muestra a bordo, y la imprenta de los datos.

INTRODUCTION

In a series of recent papers, Lasker (1975, 1978, 1979) described the importance of particle size and concentration with depth and area in relation to particulate feeding by anchovy larvae. These studies showed that information on the distribution of particles of about 20-40 μm in "effective diameter"[2] could be related to survival of anchovy larvae and thus to the size of future year classes. The usual technique for obtaining particle size and concentration data has been by overside deployment of a hose and submersible pump. This required considerable ship time and manpower. Using a pump, particle size and concentration could only be obtained by retrieving some of the water from specific depths and by counting particles suspended in the water with a Coulter Counter in the shipboard laboratory. This tedious procedure provides very few data points in vertical transects, nor does it give information on patchy distribution of particles. It became evident in our work that a method was needed that could provide for a continuous record of particle size and concentration with depth quickly and at finer depth intervals. A microprocessor-based system with a free-fall probe was designed by Brown (1977) to collect this information. This paper describes recent engineering innovations of the system, a field test under sea-going conditions, and laboratory calibration.

OPERATION

We have called this instrument a free-fall particle counter (FFPC), althrough it is tethered with a conducting cable to relay information to a dedicated microprocessor aboard the ship. The instrument is designed to resolve particle layers of at least 0.2 m thick in a vertical profile to 100 meters. In operation, the entire procedure, including deployment of 100 m of conducting cable and retrieval, takes about three to four minutes, although the actual data collection occurs in a pre-set 100 seconds during the fall of the probe. If the probe sinks too slowly, it provides more information for each depth interval, but because the pre-set 100 seconds may have elapsed too soon, it will not collect data to the desired depth. Sinking speed is a function of the amount of lead weight added to the bottom of the probe and a variety of uncontrollable ocean-related factors, e.g. drift and currents. In practice, a winch (Figure 1), designed specifically for the sensor probe (Figure 2) and its cable, is attached to the ship's bucket. As the sensor falls and the cable is payed out, the information obtained by the falling sensor is relayed to the microprocessor where it is stored on tape and displayed on a video screen as particle concentration by size of particle and depth in addition to a time and date record

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[1] Mention of trade names does not imply endorsement by the National Marine Fisheries Service.
[Manuscript received 17 January 1980.]

[2] Particles, regardless of shape, are counted as if they were spherical, hence sizes are recorded as "effective diameters."

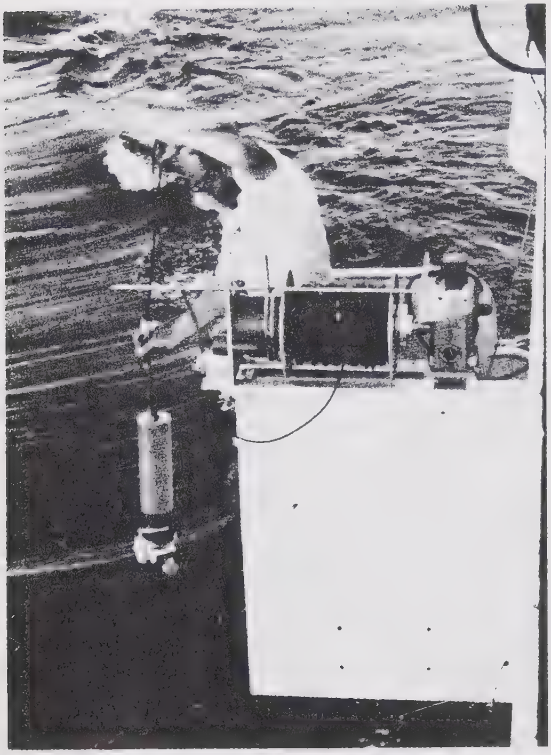

Figure 1. Sensor probe and winch for free-fall particle counter (FFPC). Winch is equipped with manual level wind and clutch. Operator is standing in ship's bucket.

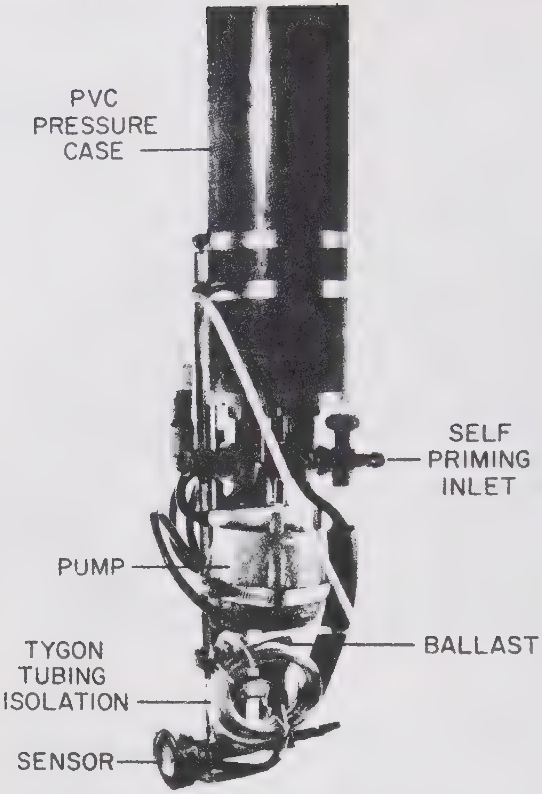

Figure 2. Free-fall particle counter (FFPC) sensor probe (after Brown 1977).

(Figure 3). The video display provides an immediate assessment of the drop and informs the operator whether or not the cast needs to be repeated. The microprocessor is programmed to accept and record the data on a cassette tape, then to relay the information from each cast to a Hewlett Packard 9825 mini-computer, which in turn is programmed to print the information in graphic form by size concentration and depth. For each cast, as many as seven particle size ranges and concentrations can be obtained with depth, and each size range and concentration can be printed on a separate graph aboard ship. Similarly, a digital output is available either of all the data collected or averaged for specified depth intervals (e.g. 1 m, 5 m, etc.).

A fine hole drilled into a fiberglass disk suffices for the sensor pore intake. We have found that a pore of 400-μm diameter can provide information on particles ranging in size from 20 to 100 μm in effective diameter. Other size pores can be used but have not yet been tested and are not reported on here. Clogging of the 400-μm pore is rarely a

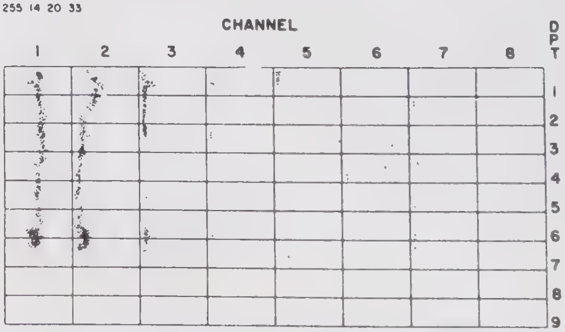

Figure 3. Diagram of a typical video display. Depth (DPT) is given on the ordinate. Day of the year (255) and time of day are shown on the screen at the upper left hand corner. Each dot is an indication of the number of particles of a particular size class sensed by the probe for 0.2 second. Channel 1 is not used because of electrical interference. With a 400 μm pore, Channel 2 receives impulses from particles ranging in effective diameter from 20.2-25.3 μm; Channel 3, 25.4-31.9 μm; Channel 4, 32.0-40.2μ m; Channel 5, 40.3-50.7 μm; Channel 6, 50.8-63.9 μm; Channel 7, 64.0-80.5 μm; Channel 8, 80.6-100.0 μm. The data from this cast are shown as a cumulative curve, third from the left in Figure 6.

problem since the amount of water pulled through the pore during any one descent is about 50 ml and usually has very few large particles in it.

CALIBRATION

Figure 4 illustrates a laboratory calibration of the sensor probe against the Coulter Counter model T_A using a mature culture of the dinoflagellate, *Gymnodinium splendens*, or 30-40 μm polystyrene beads. When particle concentrations are below 250-300 particles/ml, there appears to be no coincidence of counts, and particle concentrations can be obtained directly without resorting to a calibration curve. There is an obvious coincidence problem above 300 particles/ml, and corrections must be made whenever this is encountered. However, rarely are such high concentrations of particles >20 μm diameter found in California waters.

FIELD TEST

A typical series of casts were taken about 10 miles off the coast of San Diego on 12 September 1979 in rapid succession. Each cast and retrieval took about five minutes with the ship drifting slightly southeast. The positions of the ship are shown in Figure 5, top. There was a sharp thermocline between 7 and 18 m and a strong pycnocline at 12 m (S = 33.5 °/₀₀, T = 15.5°C; Figure 5, bottom). Figure 6 is a summary of total particles from 20-100 μm in effective diameter with depth taken at approximately 5-minute intervals. Note that the pycnocline at 12 m effectively marks the lowest boundary of a broad particle layer in the surface water. Reproductions of the computer printout are given in Figure 7. With slight changes

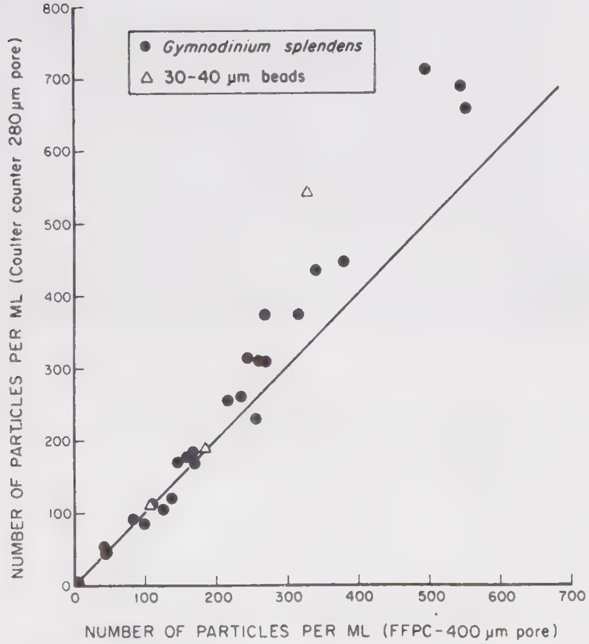

Figure 4. Calibration of free-fall particle counter (FFPC) with 400 μm pore against Model T_A Coulter Counter, 280 μm pore. Microscope counts were used to verify Coulter Counter output.

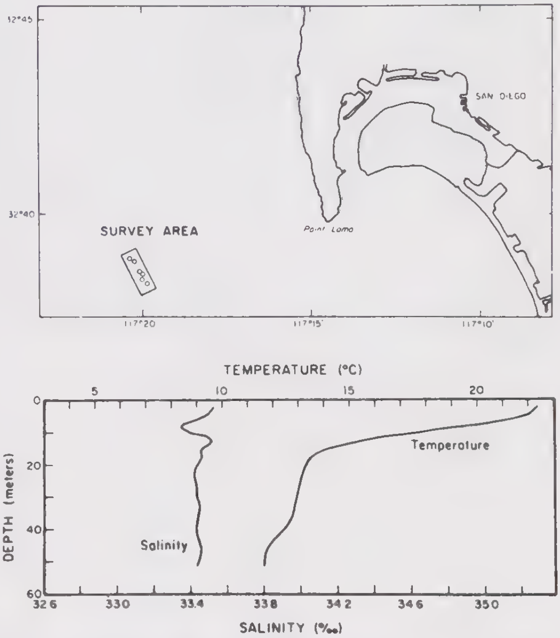

Figure 5. Top, ship positions for repetitive free-fall particle counter (FFPC) sampling; bottom, salinity and temperature profiles taken at first station.

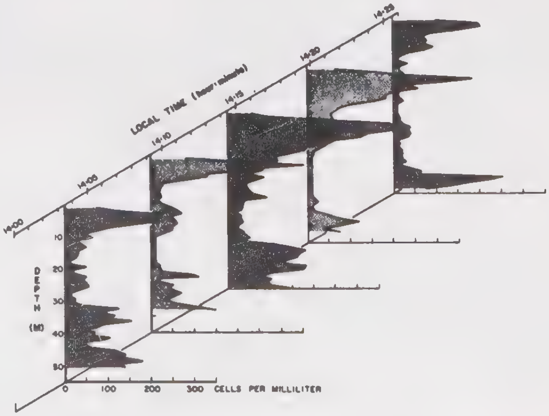

Figure 6. Total particles from 20-100 μm effective diameter with depth taken at approximately 5-minute intervals. Ship positions are shown in Figure 5.

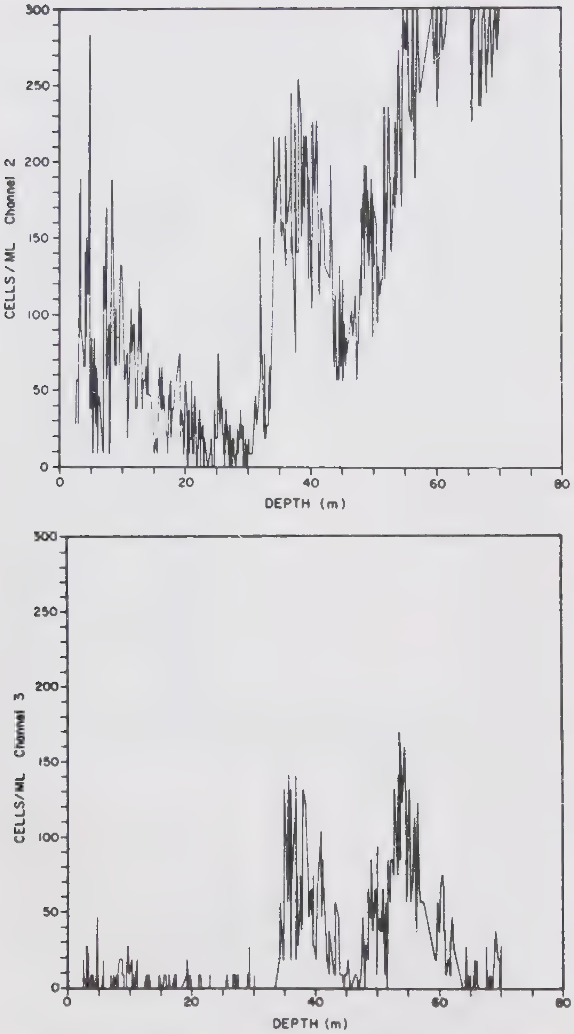

Figure 7. Graphic output from a single cast using the Hewlett Packard 9825 mini-computer and peripheral unit: Top, Channel 2, 20.2-25.3 μm; bottom, Channel 3, 25.4-31.9 μm particles.

in the Hewlett Packard 9825 program, specific size ranges can be printed separately or summed to give cumulative size ranges and concentrations with depth.

DISCUSSION

There are several operational advantages unique to this instrument. These are 1) each profile of particle concentration with depth to 100 m can be made in less than five minutes; 2) particle sizes may be differentiated by seven usable electronic channels; the size displayed in each channel may be varied by using different pore sizes; 3) an immediate plot of particle concentration by size and depth is available on shipboard by interfacing the microprocessor with a mini-computer (Hewlett Packard 9825) and its peripheral plotter and printer; 4) the submersible portion of the unit is portable and replaceable; and 5) the water drawn through the pore (about 50 ml) can be retrieved from the intake tube and preserved for later study.

Two major disadvantages to the instrument are evident: 1) species of phytoplankton and microzooplankton cannot be assigned to a particular depth; and 2) intake volumes with pores to 400 μm are small for any single cast, thus large particles (>100-μm diameter) are sampled too infrequently for statistical treatment.

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_____ ____. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212-230.

________. (in press). Factors contributing to variable recruitment of the northern anchvy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.

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DISTRIBUTION AND MOVEMENTS OF RISSO'S DOLPHIN, *GRAMPUS GRISEUS*, IN THE EASTERN NORTH PACIFIC

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ABSTRACT

Records of occurrence are summarized from 22 strandings/collections and 210 sighting records from miscellaneous sources. When available, levels of effort have been identified and utilized to interpret the trends in distribution and movement apparent from the data. Risso's dolphins occur from at least the Equator (southern end of area examined) north to approximately latitude 50° N, with regions of apparently very low density centering at about latitude 20° and 43° N. Records from northern and inshore portions of the range were most numerous during late spring through early fall. Both within and among years, periods of greatest abundance for the species north of latitude 43° N, near Monterey Bay, California, and over the southern California continental borderland appear to correspond with protracted periods of warm water. Groups contained from 1 to an estimated 220 animals, about a geometric mean of 10.7. An estimated 76.4% of the groups contained fewer than 20 animals.

The Risso's dolphin or gray grampus, *Grampus griseus*, is widely distributed in tropical and temperate waters around the world. It occurs on the western side of the Atlantic Ocean from at least Newfoundland (approximately lat. 50° N, Leatherwood et al. 1976) south to Cape Horn (approximately lat. 53° S, Norris[6]), and in the Gulf of Mexico (True 1885; Gunter 1954; Paul 1968) and the Caribbean (Caldwell et al. 1971). On the eastern side of the Atlantic it occurs from the Shetland Islands, Scotland (Turner 1892), south to the Cape of Good Hope (approximately lat. 34° S, Barnhard 1954), including the North Sea (Schultz 1970), and throughout the Mediterranean Sea complex (Bazzauti 1910; Tamino 1953; Pilleri and Gihr 1969), including the Adriatic (Trois 1883; Ninni 1901; Carrucio 1906; Riedl 1965; Pilleri and Gihr 1969). It also occurs in the Red Sea (Hershkovitz 1966) and in the Indian Ocean (Ellerman et al. 1953; Weber 1923), at least to the Indo-Australian Archipelago, and on the west side of the Pacific Ocean from the Commander Islands (approximately lat. 55° N, Sleptsov 1961) south to New Zealand (Hector 1873; Parker 1934; Alpers 1960; Gaskin 1968; Baker 1974), including the South China Sea, the Philippine Sea (Baker 1974), and the waters around the New Hebrides (Maxwell 1952), the Solomon Islands (Dawbin 1966), and New Guinea (Gaskin 1972). On the eastern side of the Pacific it has been reported from the Bering Sea (Clark 1945) and British Columbia (Guiguet and Pike 1965) south to Valparaiso, Chile (Aguayo 1975), and Cape Horn (Norris see footnote 6), including the Gulf of California (Leatherwood et al. 1979). That Risso's dolphins are present in Hawaiian waters as well is indicated by three sightings and a stranding on Maui in 1977 (E. W. Shallenberger[7]). Davies (1963) remarked on the species' overall distribution that it is basically tropical but extends its ranges poleward to overlap the ranges of temperate forms, though they generally do not penetrate so far into high latitudes. In all areas, the species' distribution is known only from infrequent stranding records and at-sea sightings, and published accounts continue to restate those records, often without adding substantial new data. Details of the animal's distribution and movements are not reported. This paper reviews the information available through 1975 on Risso's

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[6] Norris, K. S. 1968. Cruise report of the R/V *Hero*, November 12-December 11, Valparaiso-Puntarenas, Chile, 11 p. Coastal Marine Laboratory, University of California, Santa Cruz, CA 95060.

[7] E. W. Shallenberger, Curator, Sea Life Park, Waimanalo, HI 96795, pers. commun. to Leatherwood September 1977.

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dolphins in the portion of the eastern Pacific from the Equator and long. 145° W north and east respectively, from strandings, collections, and sighting records, and examines the data for patterns in distribution, movement, and seasonal occurrence.

METHODS

Inherent in the approach to this paper is the opinion that for this as for other areas, there are numerous scientists and organizations which have small amounts of information of little significance alone, but when the data are combined, they can yield a better understanding of what is known about a given cetacean species (e.g., see Leatherwood and Walker (1979) on *Lissodelphis borealis*).

We reviewed previously published records of at-sea sightings of Risso's dolphins in the study area (Table 1). We then examined over 250 previously unpublished reports of sightings of the species in the area from 1958 to 1975[8] for reliability of identification. Interviews with observers and photos assured us of the accuracy of most records. Descriptions of animals with slate gray to nearly all-white coloration, extensive scarring, a bifurcated melon, and a prominent dark dorsal fin, all distinctive characteristics of Risso's dolphins (Figure 1), aided in verification of the remainder. We discarded questionable records.

Many of the reports included estimates of herd size. Since many of these were stated as ranges (e.g., 30-40 animals), we used the midpoint of each estimate. If the estimate was such that the midpoint was a half number (e.g., an estimate of 10-15 animals) we took the lower of the numbers (e.g., 12).

Some records also included measurements of sea surface temperature at or near the location of the observation. The few of those most important to interpreting apparent trends in the more northern portions of the study area were used, along with annual summaries of temperature trends.

Incidental sighting records alone cannot be used to reliably determine trends in distribution, movements, or abundance. Data on sighting effort are essential. Although a few major marine surveys have been conducted in the study area, effort is difficult to quantify for most other sources of

TABLE 1.—Previously published at-sea sightings of Risso's dolphins in the eastern North Pacific. In the few cases where collections were reported, as in Orr (1966), herds from which animals were collected are not included as sight records.

Source	Date	Location	Number in school
Hubbs (1960)	? 1960	Isla Guadalupe, Mexico	Unreported
Fiscus and Niggol (1965)	16 Mar. 1958	38°30′ N, 124°15′ W	"Many animals"
Guiguet and Pike (1965)	22 July 1958	50°00′ N, 145°00′ W	1
Fiscus and Niggol (1965)	27 Jan. 1959	36°45′ N, 122°33′ W	3
Fiscus and Niggol (1965)	4 Feb. 1959	35°12′ N, 122°05′ W	50+
Fiscus and Niggol (1965)	8 Feb. 1959	35°44′ N, 122°43′ W	2
Fiscus and Niggol (1965)	18 Mar, 1959	41°42′ N, 125°53′ W	10+
Fiscus and Niggol (1965)	28 Mar. 1959	40°52′ N, 125°19′ W	5
Guiguet and Pike (1965)	11 Oct. 1959	50°00′ N, 145°00′ W	6
Guiguet and Pike (1965)	15 Aug. 1960	50°00′ N, 145°00′ W	5
Guiguet and Pike (1965)	4 Sept. 1960	50°00′ N, 145°00′ W	4
Daugherty (1972)	? 1971	Midway between San Diego (Pt. Loma) and San Clemente Island, Calif.	50
Leatherwood et al. (1972)	? 1971	05°00′ N, 87°04′ W	Unreported
Leatherwood et al. (1972)	? 1971	11°00′ N, 109°30′ W	Unreported
Leatherwood et al. (1979)	13 Feb. 1974	24°52′ N, 108°58′ W	5-10
Leatherwood et al. (1979)	13 Feb. 1974	28°21′ N, 112°30′ W	2

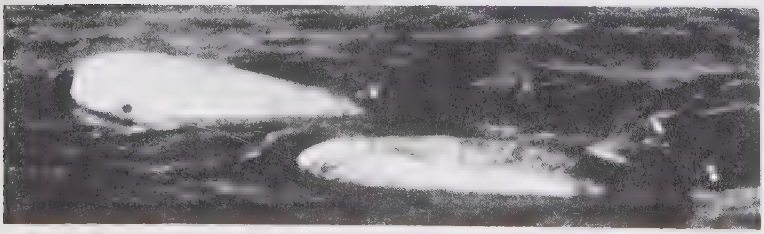

FIGURE 1.—Risso's dolphins off southern California, 1973. The animal's distinctive whitish head (in adults), scarring, and high subtriangular dorsal fin enhance the reliability of "incidental" observational records. (Photo by G. E. Lingle, courtesy Naval Oceans Systems Center, San Diego, Calif.).

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[8] A summary of verified records of observations of *Grampus griseus* in the northeast Pacific is available from Leatherwood or Perrin.

data. The following information on effort, from which we feel reliable trends may be determined, exists for the survey programs in the study area.

From San Diego to Equator—National Marine Fisheries Service (NMFS) observers, aboard tunaboats working primarily out of San Diego, Calif, surveyed the area from San Diego south to the Equator from 1966 through 1975. The majority of effort was concentrated in January and February, declining rapidly through April to no effort in the Commission Yellowfin Regulatory Area (CYRA) of the Inter-American Tropical Tuna Commission by the third quarter (Figure 2). It is evident that there has been very little effort in the nearshore portion of the tropical CYRA during the third and fourth quarters, although there were six chartered cruises between September and December. Far-offshore fishing and research activity continued throughout the year. Because the vessels return north to San Diego, running anywhere from 12 mi offshore to beyond the continental shelf off Baja California, effort appears to have been adequate throughout that area to detect major seasonal changes in composition of marine mammal fauna. This is the only program for the area for which extensive and quantified data on effort and sightings were available.

Since 1968, cruises of the Naval Ocean Systems Center, San Diego (NOSC, formerly Naval Undersea Center), have examined the continental shelf area off northwestern Baja California during winter and spring (October-December and February-April). Vessels of the Scripps Institution of Oceanography with marine mammal observers aboard have cruised extensively among the San Diego-Guadalupe Island-Cedros Island triangle for over 30 yr.

Southern California Continental Borderland—Survey effort has been extremely heavy over the continental shelf from Ensenada north to Point Conception. Norris and Prescott (1961) reported on activities of Marineland of the Pacific, primarily between Catalina and Santa Barbara Islands and the mainland shore near Los Angeles. Leatherwood (1974), Evans (1975), and Leatherwood and Walker (1979) summarized NOSC aerial

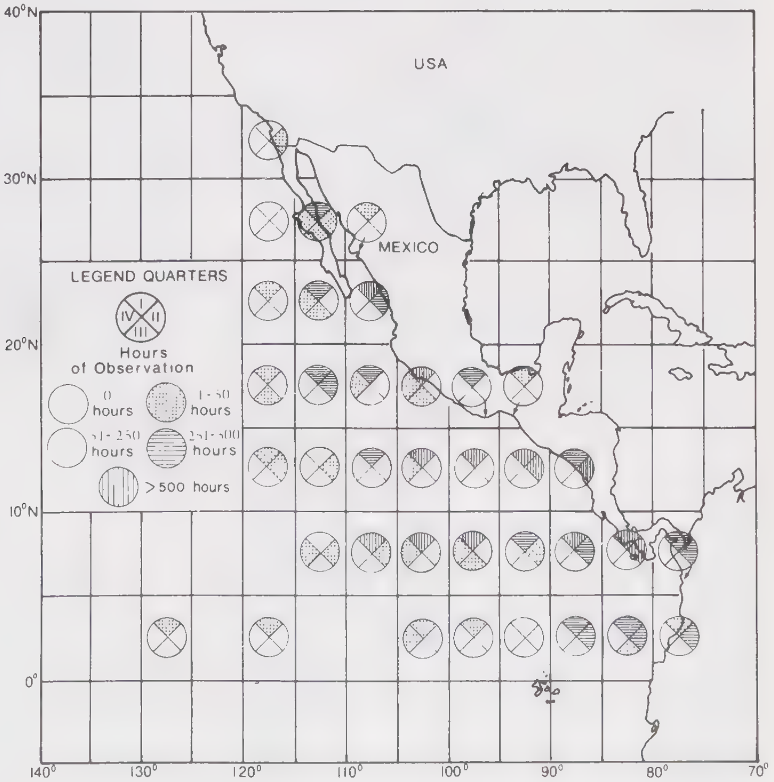

FIGURE 2.—Relative numbers of hours of observation by NMFS/SWFC observers aboard tunaboats in the eastern tropical Pacific by quarter of year, 1974-75.

and ship survey effort in this area for 1968-75. Norris et al.[9] summarized Bureau of Land Management (BLM) aerial and ship surveys during 1975 and 1976. Although variable by month, we consider this combined effort adequate at all seasons to have detected trends in composition of marine mammal fauna for the borderland and adjacent continental slope. Coverage was particularly thorough for the area in 1975, when NOSC and BLM programs overlapped.

Offshore Southern and Central California—During 1967 and 1968, cruises of the Smithsonian Institution's Pacific Ocean Biological Survey program surveyed the outer California Channel Islands and the area from lat. 29° to 37° N and seaward to long. 126° W during all quarters of the year. Marine mammal observations by experienced personnel were logged for all cruises (R. L. Brownell, Jr.[10]).

Offshore Baja California North to Washington—More recent coverage of the area from lat. 25° N to Washington State, primarily offshore, has been provided by NMFS observers out of the Southwest Fisheries Center (SWFC) placed on commercial albacore boats. In 1971-75, observers aboard 15 working albacore boats reported marine mammal observations made between May and September from lat. 25° to 46° N (Table 2). Although the time and location of their activities varied annually with the albacore migration, coverage was generally restricted to summer and generally moved north as the season progressed.

TABLE 2.—Months during 1961-75 in which marine mammal watches were maintained aboard one or more albacore vessels (×) in the eastern Pacific (1971-75), by 5° increments of latitude. A total of 15 vessels were involved.[1-4]

Lat. (° N)	May	June	July	August	September
45-50				×	×
40-45		×	×	×	×
35-40		×	×	×	
30-35	×	×	×		
25-30	×	×	×		

[1] Laurs, R. M., and Associates. 1972. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1971 and 1972. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif., 78 p.

[2] Laurs, R. M., and Associates. 1973. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1973. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif.

[3] Laurs, R. M., and Associates. 1974. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1974. Admin. Rep. 25-74-47, SWFC, NMFS, NOAA, La Jolla, Calif.

[4] Laurs, R. M., R. J. Lynn, and R. N. Nishimoto. 1975. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1975. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif.

Nearshore Central California—Recent aircraft and ship surveys by the University of California at Santa Cruz have examined the area from about Point Conception north, with the most extensive sampling effort in Monterey Bay. Coverage near Monterey Bay has been year-round (J. D. Hall[11]). Infrequent cruises by personnel from Hopkins Marine Station and Moss Landing Marine Laboratory have examined the same area (A. Baldridge[12]).

Oregon and North—With one important exception, recorded survey effort begins to decline as one moves north from California. NMFS albacore-boat observer programs conducted in the summer have extended north of Point Conception (Table 2), and one NOSC marine mammal cruise was conducted from San Diego to Kodiak, Alaska, in April 1971. The primary effort, however, including extensive coverage of the area from Seattle north through the Gulf of Alaska and northwest to the Aleutian Islands and the Bering Sea, has been that by cruises of the NMFS Northwest and Alaska Fisheries Center (NWAFC) Pelagic Fur Seal Research Program. Over the past 10 yr, these cruises have primarily spanned the fall and winter months (C. H. Fiscus[13]). Other research cruises by NWAFC have begun in the Seattle area and worked south to southern California in January, February, and March (Fiscus and Niggol 1965), while still others beginning in San Francisco have worked south to the Revillagigedo Islands in winter and spring (Rice 1963a, b).

The remainder of the sighting effort for the northeastern Pacific is difficult to assess, though it is clearly sporadic and has concentrated on coastal regions near population centers.

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[9] Norris, K. S., T. P. Dohl, R. C. Guero, L. J. Hobbs, and M. W. Honnig. 1976. Cetaceans; numbers, distribution, and movements in the southern California Bight. 192 p. Draft report to Bureau of Land Management, OCSEAP, from Coastal Marine Laboratory, University of California, Santa Cruz, CA 95060.

[10] R. L. Brownell, Jr., U.S. National Museum of Natural History, National Fisheries and Wildlife Laboratory, Wash., DC 20560, pers. commun. to Leatherwood June 1975.

[11] J. D. Hall, U.S. Fish and Wildlife Service, Office of Biological Services, 800 A Street, Suite 110, Anchorage, AK 99501, pers. commun. to Leatherwood August 1975.

[12] A. Baldridge, Library, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Fla.; present address: Hopkins Marine Station, Pacific Grove, CA 93950, pers. commun. to Leatherwood 1975.

[13] C. H. Fiscus, Northwest and Alaska Fisheries Center Marine Mammal Division, NMFS, NOAA, 7600 Sand Point Way NE Seattle, WA 98115, pers. commun. to Leatherwood June 1976.

The areas of coverage of the most important programs considered in this report are summarized in Figure 3. (The expanded area coverage of the SWFC tunaboat-observer program is shown in Figure 2).

RESULTS

Strandings and Collections

As nearly as we can determine, 22 strandings and/or collections of specimens of *G. griseus* have been recorded in the northeastern Pacific since about 1872 (Figure 4).

1. (Published). In the late 19th century, probably in 1872, although the exact date is undeterminable, Charles M. Scammon obtained two lower jaws from Monterey, Calif. (Scammon 1874). Dall (1874) used these two lower jaws as the basis for his description of *G. sternsii*, later rejected as a species by True (1889) because it was indistinguishable from *G. griseus* (G. Cuvier 1812). One lower jaw and two teeth were deposited in the U.S. National Museum (USNM 13021), though True could not make his measurements agree with Dall's and tentatively said that it was "apparently neither the No. 1 nor the No. 2 of Mr. Dall's description" (True 1889). The whereabouts of the second mandible or, if True's

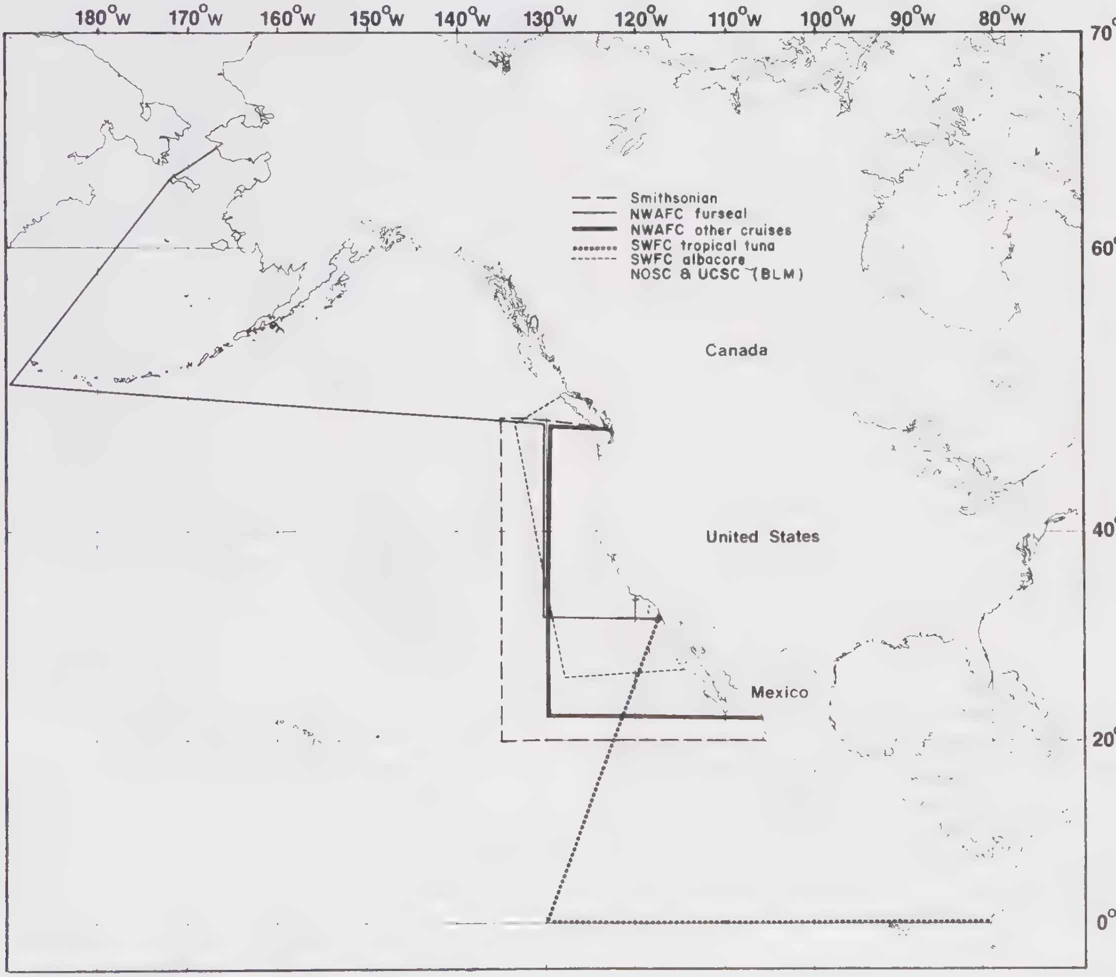

FIGURE 3.—The eastern North Pacific north of lat. 15° N, showing areas surveyed by major marine mammal survey programs (1958-75). See text for details of documentation.

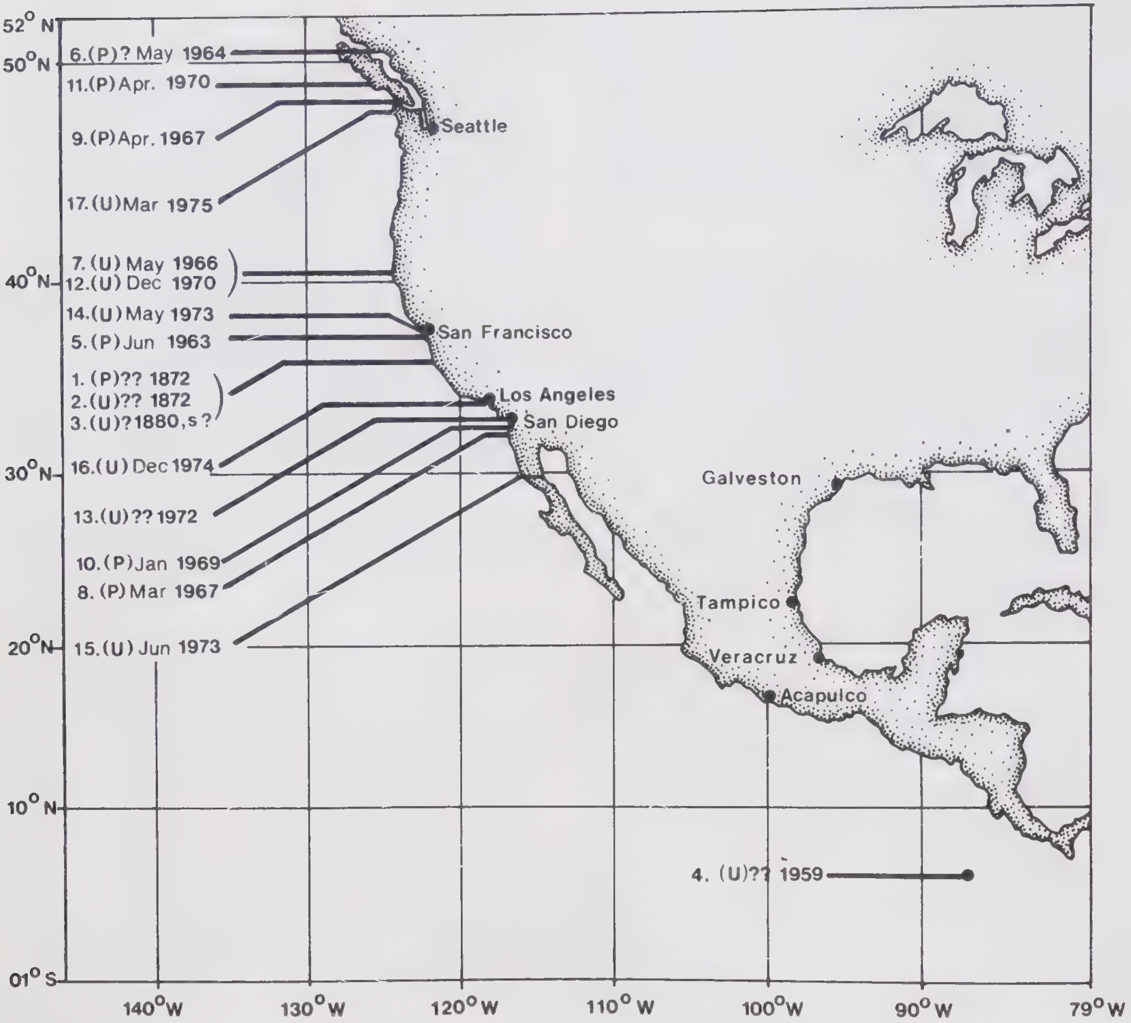
52° N
50°N
6.(P)? May 1964
11.(P)Apr. 1970
9.(P)Apr. 1967
17.(U)Mar 1975
Seattle
40°N
7.(U) May 1966
12.(U) Dec 1970
14.(U)May 1973
5.(P)Jun 1963
San Francisco
1.(P)?? 1872
2.(U)?? 1872
3.(U)?1880,s?
Los Angeles
San Diego
30°N
16.(U) Dec 1974
Galveston
13.(U)?? 1972
10.(P)Jan 1969
8.(P)Mar 1967
Tampico
20°N
15.(U) Jun 1973
Veracruz
Acapulco
10° N
4. (U)?? 1959
01° S
140°W
130°W
120°W
110° W
100°W
90° W
79° W

FIGURE 4.—Dates and approximate locations of strandings and collections of Risso's dolphins in the eastern North Pacific (1972-75) numbered in chronological order. The letters in parentheses indicate whether the record has (P) or has not (U) been previously published.

observations are correct, both mandibles described by Dall, are unknown, as is the identity of USNM 13021.

2. (Unpublished). During the same period, exact date also undeterminable, Scammon collected a second specimen which he also forwarded to True at the U.S. National Museum (USNM 21163). Like the first, this specimen was reportably taken in Monterey Bay, Calif. (C. H. Gilbert[14]).

3. (Unpublished). There are three remaining specimens from the Pacific coast of North America in the collection of the U.S. National Museum. One (USNM 28066) was purchased from fishermen in Monterey; one (USNM 49895) was taken from an unidentified locality in California; and the third (USNM 49347) was collected by C. H. Gilbert, presumably also in Monterey. Interestingly, in referring to this last specimen in his correspondance with Dall, Gilbert (see footnote 14) wrote "In addition to that, I have the complete skeleton of a calf about 6 months old. The species is abundant in Monterey

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[14] C. H. Gilbert undated letter to W. Dall, in possession of Hubbs.

Bay and additional specimens could be secured for you if you desire."

4. (Unpublished). In 1959, a single lower jaw identifiable as that of a Risso's dolphin was brought to Hubbs from Isla de Coco ("Cocos Island"), lat. 05°32′ N, long. 87°04′ W. The location of the specimen is currently unknown.

5. (Published). On 11 June 1963, a 325.0 cm male apparently dead from gunshot wounds stranded on the beach 0.9 km from Princeton by the Sea, San Mateo, Calif. The account of the stranding and its workup includes a description of the specimen, analysis of stomach contents, miscellaneous external measurements and organ weights, and some cranial measurements (Orr 1966). The specimen was deposited in the collection of the California Academy of Sciences, San Francisco (CAS 13461, Orr 1966). This account represents the first continental eastern Pacific record of the species published since the late 19th century.

6. (Published). In May 1964, a single 11-ft (334.0 cm) Risso's dolphin was observed alive in Big Bay on the west side of Stuart Island, British Columbia (approximately lat. 50°20′ N, long. 125°00′ W). The animal was shot, dissected, and discarded. The caudal peduncle and flukes were later recovered and placed in the collection of the British Columbia Provincial Museum (BCPM 9077). The animal was reported by the collectors to have been feeding on squid and to have had a heavy intestinal parasite load (Guiget and Pike 1965).

7. (Unpublished). On 13 May 1966, Robert E. Jones (Museum of Vertebrate Zoology, Berkley, Calif.) found a long dead but complete carcass of a stranded male approximately 10 km south of Cape Mendocino, Humbolt County, Calif. The total length of the specimen was 9 ft 7.5 in (293.9 cm). The skull and left flipper were collected and deposited at the Humboldt State University (HSC-66-4).

8. (Published). On 18 March 1967, an adult male stranded alive at Cantomar (Rosarita Beach), 42 km south of Tijuana, Baja California, Mexico (approximately lat. 32°18′ N, long. 117°00′ W). It was taken to Sea World in San Diego, Calif., where it survived for a short time. A photo of this animal appeared in the *San Diego Union* 28 March 1967 on page B-5. This specimen was 307.0 cm long (Harrison et al. 1969) and weighed 850 lb (386 kg) (measured by Hubbs). Although the specimen was reportedly deposited in the San Diego Natural History Museum, the Museum has no record of the specimen and its whereabouts are unknown.

9. (Published). On 20 April 1967, a 258 cm male apparently dead from a gunshot wound in the head was found stranded at Makkaw Bay, Wash. (lat. 48°19′ N, long. 124°40′ W). The dolphin had been dead an estimated 1 mo. Its stomach contained squid beaks and fragments. The skull and postcranial skeleton were preserved in the collection of NWAFC, NMFS, NOAA, Seattle, Wash. (Stroud 1968).

10. (Unpublished). On 21 January 1969, a 309 cm adult male stranded alive at Imperial Beach, San Diego County, Calif. The animal was taken to Sea World, San Diego, where it died the night of 21-22 January 1969. The complete skeleton was collected by Raymond M. Gilmore and deposited in the San Diego Natural History Museum (SDNHM 21554) (R. M. Gilmore[15]).

11. (Published). On 17 April 1970, a 266 cm male washed ashore on the east side of Vargas Island, British Columbia (lat. 49°10′ N, long. 125°58′ W). The skull, axial skeleton, and bones from one pectoral appendage were collected and placed along with a complete photo series (Photofile No. 51) in the collection of the Vertebrate Museum, Department of Zoology, University of British Columbia (UBC 9464). The report of the stranding includes external measurements, organ weights, and an analysis of stomach contents (Hatler 1971).

12. (Unpublished). On 26 December 1970, a male neonate was collected from the beach in Shelter Cove, Humboldt County, Calif. The entire specimen (Field No. WJH 71-1) was deposited at the Humboldt State University (HSU 1620) (W. J. Houck[16]).

13. (Unpublished). In August of 1970, responding to a radio call from local fishermen, F. Brocata and B. Falcone of Marineland of the Pacific investigated a call about an "albino" pilot whale which had been harpooned by fishermen between Santa Cruz and Santa Rosa Islands, Calif. When Marineland's research boat, the MV *Geronimo,* approached the whale, which turned out to be a Risso's dolphin, the animal managed to

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[15] R. M. Gilmore, Research Associate, San Diego Natural History Museum, San Diego, CA 92112, pers commun. to Leatherwood 1975.

[16] W. J. Houck, Humboldt State University, Arcata, CA 95521, pers. commun. to Leatherwood 1975.

pull out the harpoon and swim away (W. A. Walker[17]).

14. (Unpublished). On 20 May 1973, an immature female was found stranded on southeast Farallon Island, off San Francisco, Calif. (approximately lat. 37°42′ N, long. 123°00′ W). The available measurements for the specimen are as follows: total length 270 cm, dorsal fin 27.5 cm, axilla-tip of flipper 5 cm, origin of flipper to tip of lower jaw 46.5 cm, anus-tip of lower jaw 178 cm, width of flukes 62 cm. The specimen was not collected (R. L. Brownell, Jr. see footnote 10).

15. (Published). On 18-19 June 1973, four females and a fifth animal of undetermined sex, all about 13 ft long (400 cm) and weighing 500-600 lb (73-77 kg) stranded alive at Punta Buffeo, Baja California, about 100 mi (160 km) south of San Felipe on the northwest coast of the Gulf of California (approximately lat. 29°55′20″ N, long 114°26′20″ W). All five animals were towed out to sea (dead), and no materials were retrieved (Leatherwood et al. 1979).

16. (Unpublished). On 8 December 1974, a female stranded alive at the Manhattan Beach Pier, Los Angeles, Calif. (approximately lat. 33°55′ N, long. 118°25′ W). The animal was alive when it was collected by Marineland of the Pacific but died almost immediately after collection. It was photographed, measured, and necropsied at the Los Angeles County Museum of Natural History, where it is currently held as specimen LACM 47145. Detailed findings will be reported elsewhere (W. F. Samaras and D. R. Patten[18]).

17. (Unpublished). On 10 March 1975, a 348 cm female stranded alive at Port Discovery, Wash., in the Strait of Juan de Fuca (about lat. 48°02′ N, long. 122°52′ W), perhaps driven ashore by killer whales. The animal was recovered alive and taken to Seattle Marine Aquarium where it died on 11 March. The complete skeleton is in the collection of the NWAFC (No. 1975-1).

At-Sea Sightings

We found 16 previously published records of at-sea sightings of Risso's dolphins for the study area (Table 1) and 194 additional previously unpublished reliable records (see footnote 8) (Figure 5). When examined by latitude (Figure 5), the distribution of sightings falls into three major groups—those from the Equator to approximately lat 20° N (Zone I); those thence north to approximately lat. 43° N (Zone II); and those north of lat. 43° N (Zone III). Zones I and II are separated by a broad region characterized by very few sightings, centering at about lat. 20° N and extending from lat. 14° to 29° N. All except two sightings in that area of low density were within 60 mi of the Mexican coast, though seaward of the continental shelf. The separation between Zones II and III is less pronounced, centering at lat. 43° N and extending from lat. 38° to 45° N.

Regarding seasonality, records in Zone I are almost exclusively limited to first and second quarters, and the majority of those from Zone III are from the period July through October. Both of these apparent seasonal fluctuations result from the biases in observation effort discussed above. Those from Zone II are distributed throughout the year. Records from north of Point Conception (lat. 35° N) are most numerous in the third quarter (Figure 6).

Off southern California (approximately lat. 31°-35° N), records from 1959 to 1975 were sporadic, reaching a peak of 11 in 1974 (Table 3). Until 1971 the majority of sightings for the area were seaward of the 100-fathom curve; however, beginning in 1971 and increasing in frequency through 1974 (9 of 11) and 1975 (3 of 3), most sightings were over the continental shelf.

Although surface water temperatures were not reported for most sightings, Risso's dolphins have been sighted in waters ranging from 28° to 10° C. Sightings in Zone I cover the full range of temperatures reported for the area. Sightings off southern California in 1974 and 1975 were associated with water temperatures above 19° C. Of the 22

TABLE 3.—Summary of sightings of Risso's dolphins off southern California (about lat. 31°-36° N), 1959-75, showing the frequency of encounter over and seaward of the continental shelf.

Year	Total no. sightings	Over continental shelf	Seaward of continental shelf
1959	1	1	0
1960	1	1	0
1965	1	0	1
1966	3	0	3
1967	9	0	9
1968	3	1	2
1971	4	4	0
1972	4	4	0
1973	3	2	1
1974	11	10	1
1975	3	3	0

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[17] W. A. Walker, 21 Barkentine Road, Rancho Palos Verdes, CA 93704, pers. commun. to Leatherwood 1975.

[18] W. F. Samaras, Research Associate, and D. R. Patten, Curator, Department of Mammals, Los Angeles County Museum of Natural History, Los Angeles, CA 90007, pers. commun. to Leatherwood 1975.

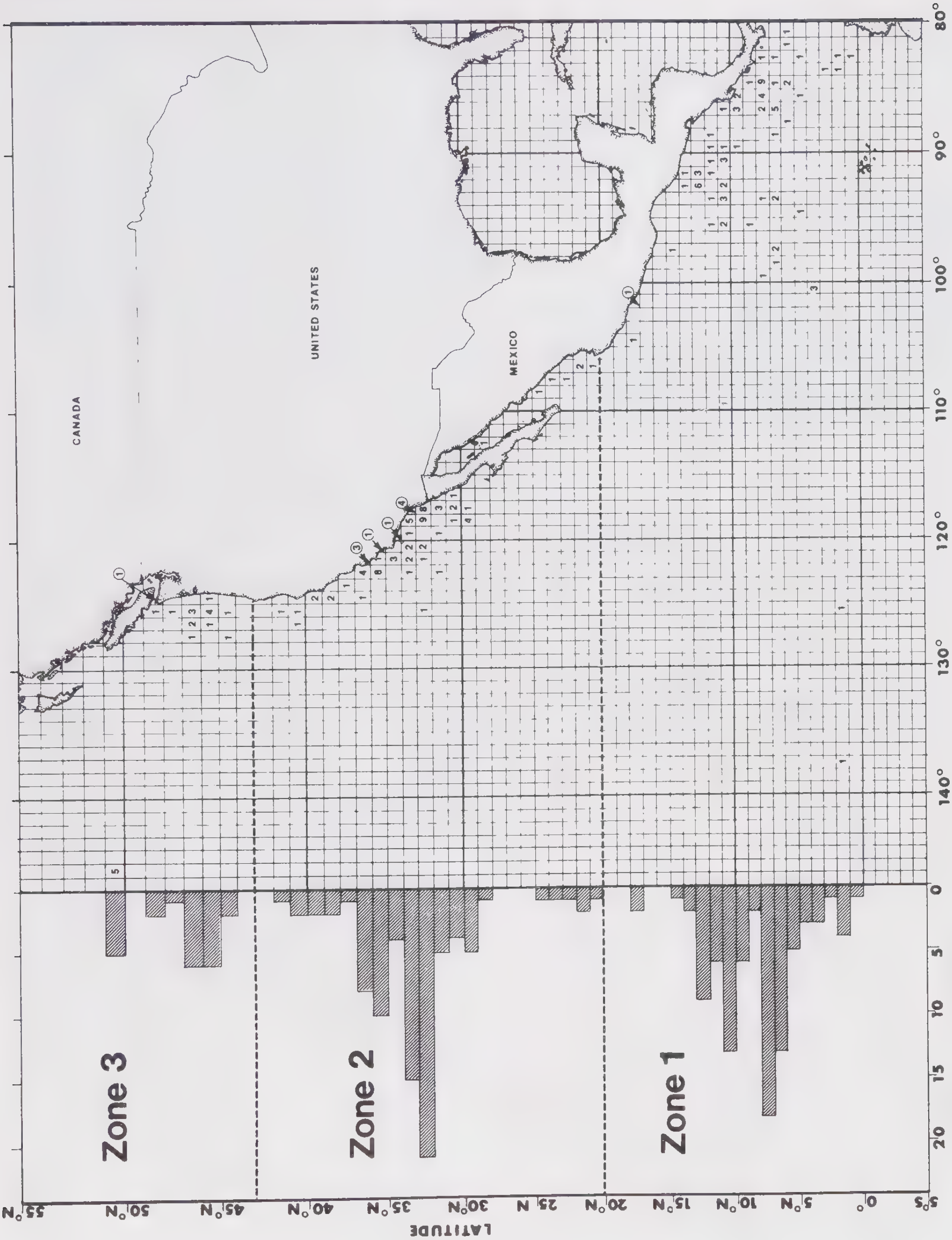
CANADA
UNITED STATES
MEXICO
Zone 3
Zone 2
Zone 1
80°
90°
100°
110°
120°
130°
140°
55°N
50°N
45°N
40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
5°S
LATITUDE
0
5
10
15
20
NUMBER OF SIGHTINGS

FIGURE 5.—At-sea sightings of Risso's dolphins in the eastern North Pacific (1958-75) by 1° square and frequency by 1° of latitude based on 210 sightings.

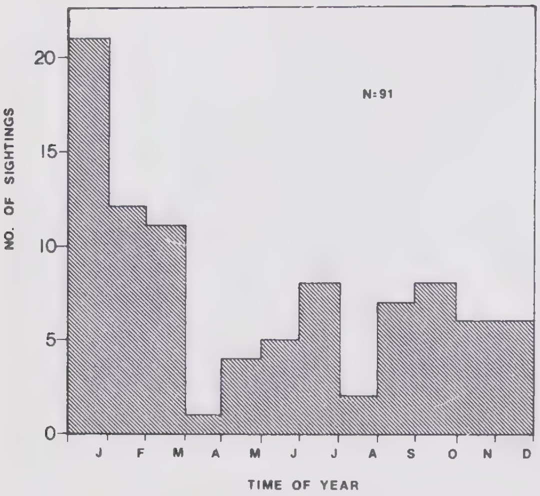

FIGURE 6.—Frequency of sightings of Risso's dolphins by month in Zone II in the eastern North Pacific (defined in Figure 5).

most northern records, the 4 from February to April were associated with water temperatures of 12° and 13° C, unusually high temperatures for the season.

Of the records, 12 published and 191 unpublished provided usable estimates of herd sizes. Numbers of animals sighted ranged from 1 to 220, about a geometric mean of 10.65. About 75% of the groups contained fewer than 20 animals (Figure 7). No statistically significant differences could be demonstrated among herd sizes from different zones (I, II, III) or different seasons (Mann-Whitney *U* Test, $\alpha = 0.05$).

SUMMARY AND DISCUSSION

Risso's dolphins are clearly abundant and widely distributed year-round in tropical and warm temperate waters of the northeastern Pacific.

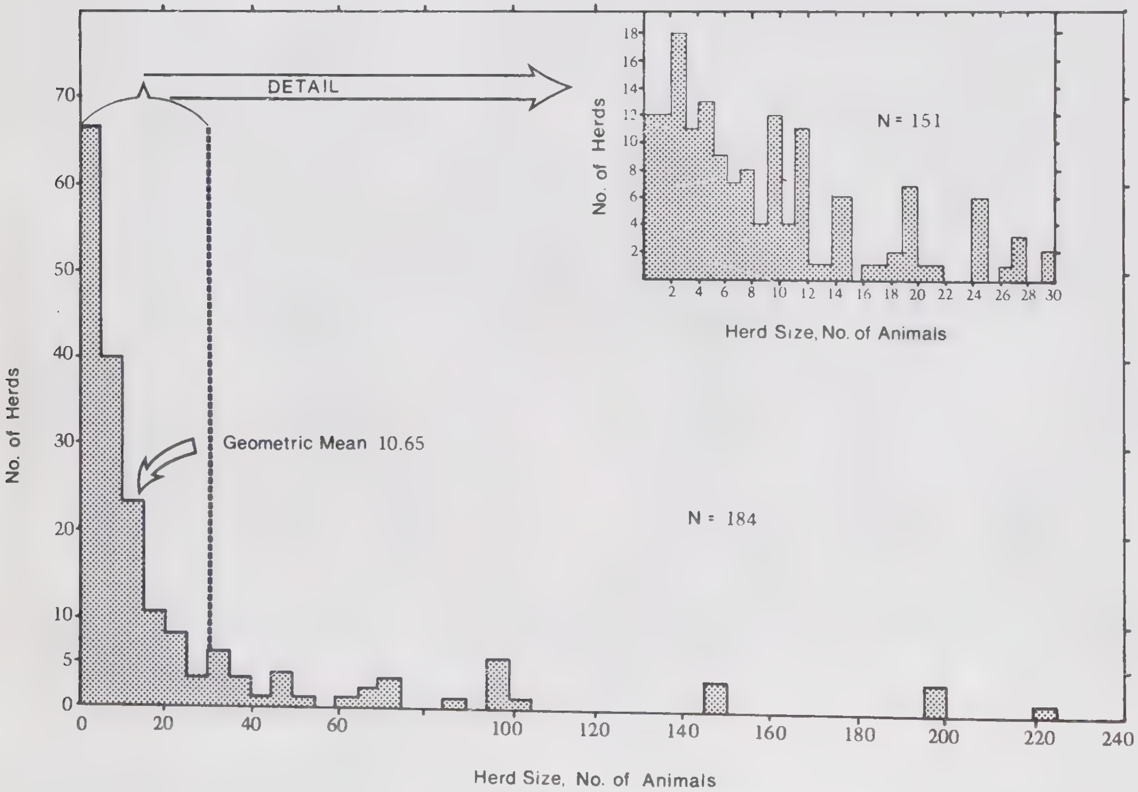

FIGURE 7.—Distribution of estimated "herd" sizes of Risso's dolphins, in the eastern North Pacific (1958-75). Inset gives detail for herd sizes with <30 animals.

The rather dramatic decrease in the number of sightings north of about lat. 13° N and the very limited number of offshore sightings in the broad belt from about the latitudes of Cedros and Guadalupe Islands south to approximately Acapulco, appear to reflect an area of apparent very low density in the species' distribution, since survey effort in the area was heavy even where no sightings were reported. Pronounced distributional gaps in portions of the same ocean area have been documented for *Delphinus delphis* (Evans 1975) and *Stenella* spp. (Perrin 1975).

Risso's dolphins appear to occur year-round in offshore waters from about central Baja California northward to about San Francisco. Movements onto the continental shelf of southern California are seasonal and appear to be related to surface temperatures. For example, records of Risso's dolphins over the continental shelf were more numerous in 1974 than in previous years since 1968, despite an equal effort, and more numerous than in 1975, despite increased survey effort in that year. In 1974 and 1975, surface temperatures were unusually high (California Cooperative Oceanic Fisheries Investigations[19]).

A poorly defined area of apparent low density in distribution, centering at about lat. 43° N, probably reflects generally poor sampling in the area from about San Francisco north to the latitude of Seattle and not any real change in the species' density there.

Records from lat. 45° to 51° N are most abundant during summer and are primarily off the continental shelf. Like the movements onto the southern California continental borderland and those into more northern latitudes, this change appears to relate to warming of surface waters.

The reports of abundance near Monterey in the late 19th century seem inconsistent with modern records of low abundance in the area. It may well be that this indication of the common occurrence of the species in Monterey Bay in the 1870's and 1880's represents a holdover of the occurrence of tropical animals in central California in the 1850's (Hubbs 1948). This being the case, the movement of Risso's dolphins north and inshore in some abundance during that period is consistent with behavior in 1974 and 1975 off southern California. Southward movements of the Dall's porpoise, *Phocoenoides dalli*, into southern California (Norris and Prescott 1961) and seasonal movements of the right whale dolphin, *Lissodelphis borealis* (Leatherwood and Walker 1979), and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens* (Leatherwood and Reeves 1978), in the eastern North Pacific have been similarly linked to seasonal changes in water temperature.

Despite extensive survey effort in the northern temperate and Arctic eastern Pacific, Risso's dolphins have not been reported north of lat. 51° N. Therefore, since it provided no new data, the summary report of the species' occurrence in the Bering Sea (Clark 1945) is of doubtful accuracy.

Considered together, these records tend to support Davies' (1963) summary of the species' distribution, at least in the northeast Pacific. It appears, as he contended, to be primarily tropical, extending its range poleward to overlap with temperate forms, though not penetrating as far into high latitudes. Perhaps the most important point supported by these records is the dynamic nature of distribution of this (and probably other) marine mammal species. In addition to well-documented short-term and seasonal movements, there appears to have been a long-term fluctuation in the boundries of species' ranges, apparently in responses to long-term environmental changes.

ACKNOWLEDGMENTS

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[19] California Cooperative Oceanic Fisheries Investigations. Unpublished data in files of CalCOFI at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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8049

Shortbelly Rockfish, *Sebastes jordani*: A Large Unfished Resource in Waters Off California

WILLIAM H. LENARZ

Introduction

The shortbelly rockfish, *Sebastes jordani*, is one of the more distinctive members of the 57 species of rockfish (genus *Sebastes*) which are reported from California waters. The species obtains its common name from the fact that its vent is about midway between the origin of the anal fin and insertion of the pelvic fin, while the vent of other species of rockfish is located farther back, much closer to the origin of the anal fin. The shortbelly rockfish also has a more strongly incised tail and a more fusiform shape than most rockfish.

Moser et al. (1977) noted that larvae of shortbelly rockfish are the longest at birth of eastern Pacific rockfish studied to date. Also, the larval period is long prior to transformation to the juvenile stage when compared with other eastern Pacific rockfish. These features, in addition to the pigmentation pattern and morphometrics of young larvae, are remarkably similar to those of the redfish or ocean perch, *S. marinus*, group of the Atlantic Ocean.

Another distinction of adult shortbelly rockfish is that it occurs in midwater and away from underwater objects such as reefs or kelp more often than most, if not all, California representatives of the genus. Occasional catches have been made by purse seiners fishing in southern California waters, and the species predominated in midwater and demersal trawl catches of rockfish off central California in the 1977 rockfish survey (Gunderson and Sample, 1980).

Shortbelly rockfish have been reported from San Benito Island, Baja California, Mexico (Moser et al., 1977) to La Perouse Bank, British Columbia (Miller and Lea, 1972). Miller and Lea also report maximum depth as 283 m (155 fathoms) and maximum total length as 305 mm (12 inches).

While there is no fishery for shortbelly rockfish, the species appears to be very abundant in California waters. Moser et al. (1977) estimated that larvae of shortbelly rockfish composed 20 percent of all rockfish larvae taken in a sampling program off southern California and 12 percent off central California in 1966. While the catch of shortbelly larvae compared with all rockfish larvae was higher off southern California than central California, the catch per standard haul was higher off central California (4.22 larvae) than southern California (2.65 larvae). The biomass in a limited area of its range, between Pt. Ano Nuevo and Pt. San Pedro, was estimated to be 295,000 metric tons (t) from the results of the hydroacoustic and midwater trawl segment of the rockfish survey) Mason[1]).

Preparation of this paper was prompted by the interest shown by both fishermen and processors in developing a fishery for shortbelly rockfish. The objectives of the paper are to summarize information on the species and: 1) Describe the biology of the species, 2) make first approximations of the reaction of the stock(s) to various levels of fishing, 3) review the rockfish survey results with regard to fishing, 4) review potential of a fishery, and 5) discuss management options for the fishery.

Biology

Larval and Juvenile Stages

Moser et al. (1977) summarized available information on larval and juvenile stages of shortbelly rockfish. The larvae are released at an average size of 5.4 mm by the ovoviviparous females between January and April. Larvae were collected between northern Baja California, Mexico, and as far north as San Francisco, Calif. Their samples were not taken north of San Francisco. While larvae were collected as far as 278 km (150 miles) offshore, all above-average catches were taken much closer to shore. They also reported that larvae metamorphose to juveniles at 27 mm and appear to begin forming schools at the surface at that time. Juveniles up to 62.8 mm have been taken by dip nets under night lights. On the other hand, specimens as small as 70 mm were taken by bottom trawling during the rockfish survey.

Growth

Shortbelly rockfish, while being one of the smaller species of rockfish, has the highest rate of growth completion (k) of 10 California species studied by Phillips (1964). The von Bertalanffy

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ABSTRACT—Shortbelly rockfish, Sebastes jordani, *appear to be abundant in California waters and present the potential for development of a new large fishery in the area. This paper contains: 1) A description of the biology of the species, 2) first approximations of the effect of fishing on the stock, 3) a review of the rockfish survey results with regard to fishing, 4) a review of the potential for development of a fishery, and 5) a discussion of management options for the fishery.*

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[1] Mason, J. E. 1978. Preliminary report on the hydroacoustic/midwater trawl survey for rockfish conducted off parts of the American and Canadian west coasts during July 12-September 30, 1977. Unpubl. manuscr., 6 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

growth curve was used to describe growth:

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where L_t = total length (mm) at t,
t = age in years,
k = growth completion rate,
t_0 = theoretical age when fish is length 0, and
L_∞ = estimate of average length attained at maximum age.

Phillips combined age-length data from both sexes and made his estimates from back-calculated lengths (estimates of length at time of formation of each annual ring on a scale) made from scale readings and measurements. He assumed that scales form at birth. My experience with several other species of rockfish indicates that scales form when the fish reach about 20 mm. Thus the back-calculations of Phillips probably slightly under-estimate lengths of young fish.

Additional data on growth are available from the rockfish survey. Otoliths from 1,081 specimens were read. Opaque zones of fast growth were just beginning to be formed at the time of sampling (midsummer). Phillips' back-calculations appear to be at the end of the growth season (midwinter). Thus fish from the rockfish survey should be 0.5 year older than those Phillips used. Phillips used total lengths, while fork lengths were measured for the rockfish survey. Total length is about 15 mm greater than fork length for shortbelly rockfish, and the survey data were adjusted accordingly. The program BGC2 (Abramson, 1971) was used to estimate parameters of the growth curve. The estimate of k for the survey data, 0.27721, is very close to the estimate by Phillips, 0.27520. The estimates of L_∞ are also close, 315 (Phillips) and 301 (survey). Comparison of the two growth curves (Fig. 1) reveals that the main differences occur at young ages. As previously mentioned, Phillips probably underestimated length of fish at young ages. Also mesh size of the nets used by the survey may have selected for relatively large fish at young ages. Phillips obtained fish from several sources and evaluation of selectivity is not possible. Data from the surveys (Fig. 2) indicated that females grow larger than males and attain maximum size at a slower rate of completion (lower k). Growth does not appear to be related to depth of capture, but there are insufficient data from the survey to arrive at conclusive results.

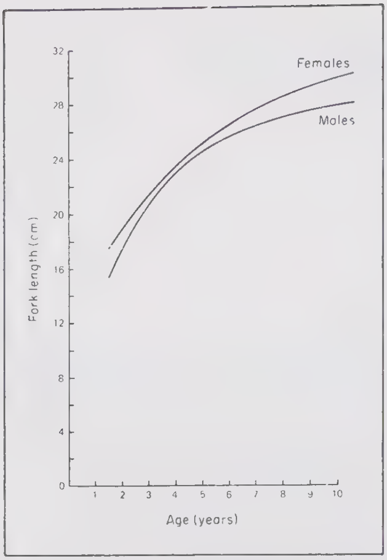

Figure 1.—Von Bertalanffy growth curves for *Sebastes jordani* estimated from this study and by Phillips (1964).

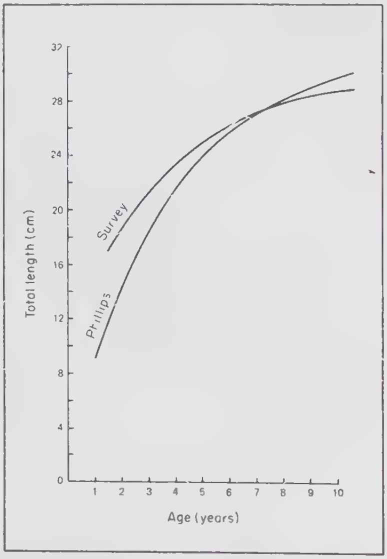

Figure 2.—Von Bertalanffy growth curves for female and male *Sebastes jordani*. L_∞ is 324 mm for females and 290 mm for males; k is 0.2112 for females and 0.2980 for males.

Length-Weight

The length-weight relationship was estimated by Phillips to be log $W = \alpha + \beta \log L$, where W = weight in pounds, L = total length (mm), $\alpha = -8.05202$, and $\beta = 3.1518$.

Maturation, Fecundity, and Sex Composition

Phillips (1964) reported that 50 percent of shortbelly rockfish " . . . are mature when 6½ inches [16.5 cm] long, or 3 years old." The fecundity-length relationship, estimated by me from Phillips' data on 10 specimens is $\ln F = \alpha + \beta \ln L$, where F = fecundity (numbers of eggs), L = total length (mm), $\alpha = -8.43523$, and $\beta = 3.30611$.

About 45 percent of the survey catches of shortbelly rockfish between 14 cm and 27 cm were males. Few of the fish larger than 27 cm were males.

Movements

While many aspects of the life history of shortbelly rockfish appear in the literature, nothing could be found on movements. Tagging studies on blue rockfish, *S. mystinus*, Miller and Geibel (1973); yellowtail rockfish, *S. flavidus*, Carlson and Haight (1972); copper rockfish, *S. caurinus*, Dewees (1970); and black-and-yellow rockfish, *S. chrysomelas*, and gopher rockfish, *S. carnatus*, Hallacher (1977) and Larson (1977) indicated little movement. However, these five species do not have strongly incised tails or fusiform bodies. These aspects of morphology would suggest that shortbelly rockfish are stronger swimmers and are better adapted to swim away from predators and/or make more extensive movements than the other five species (Hobson and Chess, 1978). Analyses of catch rates of Pacific ocean perch, *S.*

alutus, indicate considerable movement into relatively shallow waters during spring and summer and return to deeper water in the winter (Gunderson, 1972). Pacific ocean perch have more strongly indented tails and fusiform bodies than the five species that were tagged but less than shortbelly rockfish. Sorokin (1961) documented long (at least 1,112-km (600-mile)) migrations of stocks of redfish (or ocean perch), and deep-water redfish, *S. mentella*, in the Atlantic Ocean.

Data from bottom trawl catches of the rockfish survey indicate that shortbelly rockfish do make significant movements. Length and age samples were expanded to entire catches assuming that sampled fish were taken at random. Size of fish tends to increase with depth (Fig. 3). Size for a given depth stratum tends to increase in a northerly direction between lat. 34° and 39°N. Depth of capture of shortbelly rockfish also tends to increase in a northerly direction between lat. 35° and 39°N. The combined results of these trends is a very strong tendency for size to increase in a northerly direction between lat. 34° and 39°N (Fig. 4). While age composition data are not sufficient to separate effects of depth and latitude, age of shortbelly rockfish tends to increase as depth and latitude increase (Fig. 5). The age and length composition data from the rockfish survey indicate that at least during summer, shortbelly rockfish tend to move into deeper waters and to the north as they grow.

Data on larvae revealed areas of heavy spawning from Los Angeles to at least San Francisco during January 1966 and March 1975.[2] Very heavy spawning occurred off Monterey (lat. 37°N), Avila Beach (lat. 35°N), and Santa Barbara (lat. 34°N). Heaviest spawning occurred off Monterey. The heavy spawning from Los Angeles to at least San Francisco in the same month indicated that if shortbelly rockfish do tend to move north as they grow, they do not make long return migrations to the south in the winter to spawn.

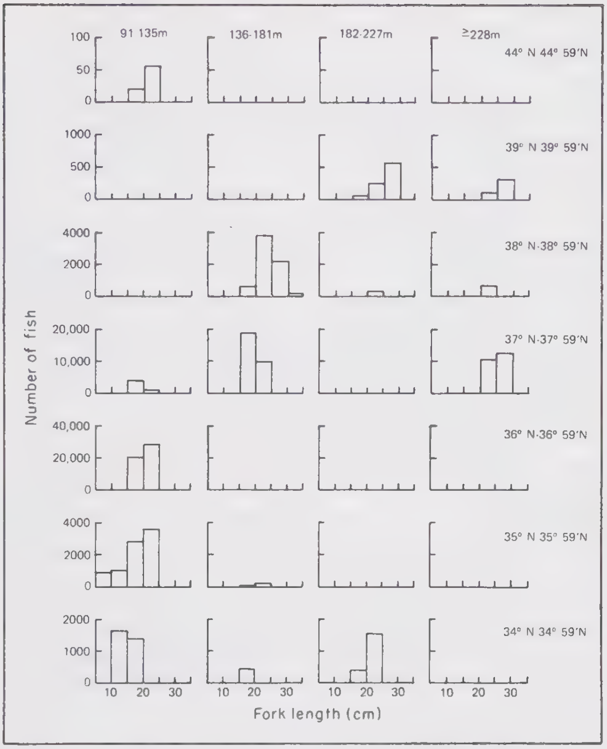

Figure 3.—Length composition of *Sebastes jordani* caught by bottom trawling during rockfish survey as a function of depth and latitude.

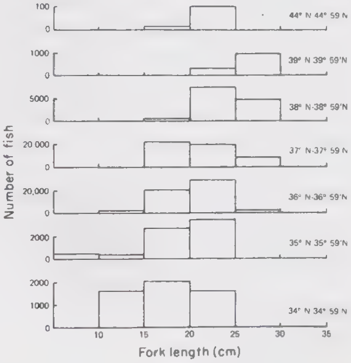

Figure 4.—Length composition of *Sebastes jordani* caught by bottom trawling during rockfish survey as a function of latitude.

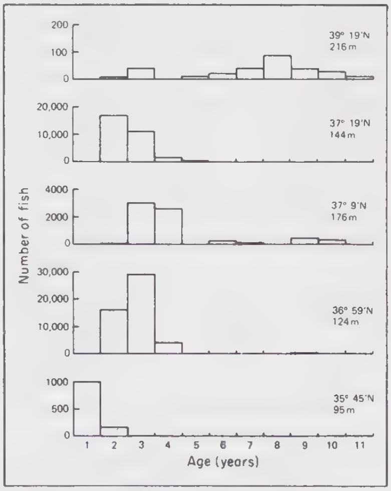

Figure 5.—Age composition of bottom trawl catches of *Sebastes jordani* during rockfish survey.

Relationships With Other Species

Shortbelly rockfish appear to be an important prey item in central and southern California. Merkel (1957) found that rockfish represented 22.5 percent of the food volume of chinook

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[2] Unpublished data of H. G. Moser, Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038. Pers. commun. 1978.

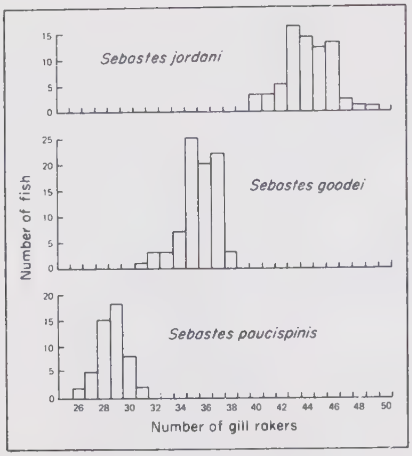

Figure 6.—Gill raker frequencies of *Sebastes jordani*, *S. goodei*, and *S. paucispinis*.

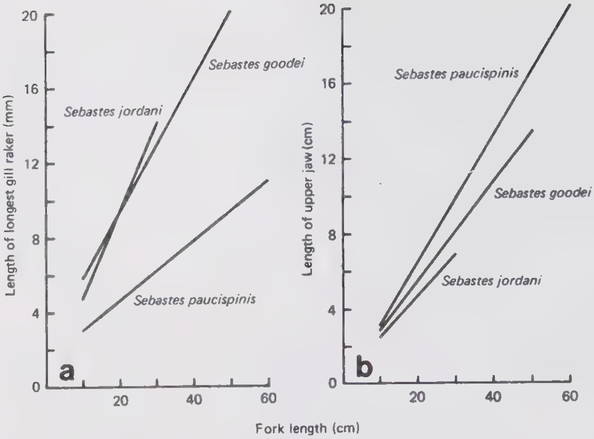

Figure 7.—Relationships between length of longest gill raker and fork length (a) and length of upper jaw and fork length (b) for *Sebastes jordani*, *S. goodei*, and *S. paucispinis*.

salmon, *Oncorhynchus tshawytscha*, off San Francisco between February and November. In June and July more than 50 percent of the food was rockfish, of which 70 percent was shortbelly rockfish. Few of the rockfish exceeded 89 mm (3.5 inches). Shortbelly rockfish less than 89 mm are probably in their first year of life. Of 78 fish sampled from pigeon guillemots, *Cephus columbia*, nesting on the Farallon Islands, two were shortbelly rockfish that were 59 and 83 mm in standard length (Follet and Ainley, 1976). Hubbs et al. (1970) reported that 4 otoliths of shortbelly rockfish were found in 498 otoliths sampled from western gull, *Larus occidentalis*, castings near San Diego. The fish were thought to have been stolen from Brandt's cormorant, *Phalacrocorax penicillatus*. Trawl-caught bocaccio, *S. paucispinis*, and chilipepper, *S. goodei*, are often seen with shortbelly rockfish protruding from their mouths, but these specimens may represent unnatural feeding within the trawl. A number of studies on food of fish, marine mammals, and birds found small rockfish to be important prey items, but did not identify the items to species. In summary, at times shortbelly rockfish can be an important prey item for chinook salmon and possibly other fish. They also compose yet undetermined portions of the diets of some birds. Only two studies reported the size of consumed shortbelly rockfish. In both cases small fish, probably less than 1 year old, predominated.

Shortbelly rockfish belong to a group of important rockfish that inhabit California waters between 50 and 125 fathoms (91 and 229 m) during adult life. The other two members are bocaccio and chilipepper, both of which are very important components of California rockfish landings. All three species are relatively fusiform and have deeply incised tails for rockfish.

Since the three species are often caught together and belong to the same genus, ecological theory requires that there be mechanisms that separate the species into different niches. Morphological features, measured following procedures of Phillips (1957), related to feeding differ considerably among the species. For example, there is almost no overlap in gill raker counts for the three species (Fig. 6). However, the relationship between length of the largest gill raker of the first arch and fork length is similar for chilipepper and shortbelly rockfish, but differs between these two species and bocaccio (Fig. 7a). There are considerable differences in the relative length of upper jaw among the species (Fig. 7b). The data presented in Figures 6 and 7 suggest that shortbelly rockfish consume the smallest organisms, probably plankton, of the three species and bocaccio consume the largest, probably fish. Phillips (1964) stated that the shortbelly rockfish " . . . feed exclusively on macroplanktonic organisms, primarily euphausids," while chilipepper " . . . may feed on euphausids and small squids, or on small fishes such as anchovies, young hake, *Merluccius productus*, and lanternfish," and bocaccio " . . . feed on smaller rockfishes, sablefish, *Anoplopoma fimbria*, anchovies, lantern-fish, and squids, *Loligo opalescens*."

A compilation of upper jaw length frequencies of the three species in rockfish survey tows containing shortbelly rockfish indicates little overlap (Fig. 8). Since young specimens of the larger species have jaw lengths of the same size as older specimens of the smaller species, the lack of overlap shown in Figure 8 suggests that the three species are distributed in a fashion that minimizes the possibility of competition for food.

First Approximation of Reaction of Species to Fishing

Yield per recruit calculations often are used to make first approximations of production of a stock under different fishing strategies. Estimates of growth

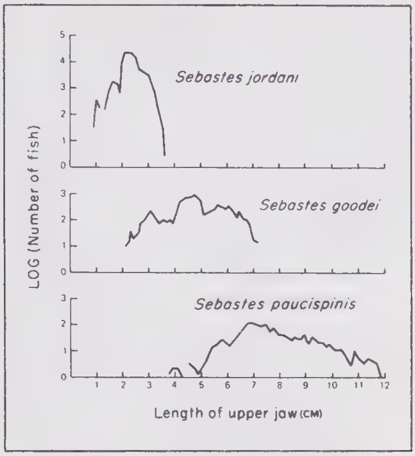

Figure 8.—Frequencies of upper jaw length of *Sebastes jordani*, *S. goodei*, and *S. paucispinis* caught in rockfish survey bottom trawls containing *S. jordani*.

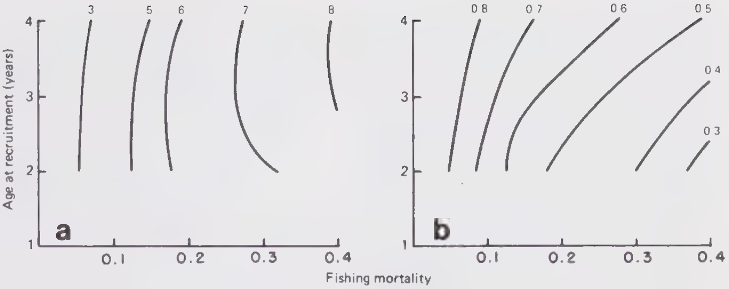

Figure 9.—Yield per recruit (a) and relative fecundity (b) (production of larvae by fished stock/production of larvae by unfished stock) of *Sebastes jordani* as functions of age at recruitment and instantaneous rate of fishing mortality (F).

and mortality are needed for the calculations. Growth estimates have already been presented. No estimates of mortality rates were found in the literature. Often the rate of natural mortality (M) is approximately equal to k (Beverton and Holt, 1959). Thus a first approximation of M is 0.275. Of 1,081 shortbelly rockfish aged from rockfish survey catches the oldest were 12 years old, which is older than the 10-year maximum age reported by Phillips (1964). It is likely that, if M is significantly lower than 0.275, older fish would occur in the samples. Indeed, a higher value of M would be reasonable.

Assuming that natural mortality is constant and that fishing mortality is constant beyond age at recruitment, I used the Ricker (1958) yield equation to estimate yield per recruit at three ages of recruitment: 2, 3, and 4 years. Results of the calculations indicate that yield per recruit is not sensitive to age of recruitment at F (fishing mortality) values less than 0.25 (Fig. 9a). When F is greater than 0.25, yield per recruit for recruitment at ages 3 or 4 is greater than when age at recruitment is 2 years. There is little difference in yield per recruit when age at recruitment is 3 or 4 for the values of F between 0.05 and 0.4.

The fecundity of shortbelly rockfish is similar to the clupeids which have a well-documented history of recruitment failures in heavily fished stocks (Murphy, 1977). With this in mind, the effect of fishing on production of larvae by a population of shortbelly rockfish was estimated. Fish were assumed to spawn once at the beginning of the year, the maturity schedule and fecundity-age relationship described in the Biology section were used, and fishing rates were assumed to be equal for males and females. The results (Fig. 9b) indicated that fishing would have a considerable effect on relative fecundity (production of larvae of fished stock/production of larvae of unfished stocks), and that relative fecundity is very sensitive to age at recruitment at higher levels of fishing mortality.

Review of Rockfish Survey Results With Regard To Fishing

Numbers of catches of shortbelly rockfish exceeding 450 kg (1,000 pounds) were made by 0.5-hour bottom and midwater trawls during the rockfish survey and a pilot survey (Gunderson and Nelson[3]) in the Monterey area during 1976 (Table 1). An area of high catches by both gears in both years was between lat. 36°56′ and 37°21′N. Large catches were made by both gears between lat. 36°18′ and 36°30′N in 1976 but not in 1977 even though nine bottom trawl hauls were made in the area in 1977. Most large midwater catches were taken by trawling close to the bottom. The midwater trawl catches averaged higher than the bottom trawl catches, 3,728 and 1,952 kg, respectively, probably because bottom trawls were set at preselected stations, while

Table 1.—Catches of shortbelly rockfish, *Sebastes jordani*, that exceeded 450 kg in one-half hour bottom and midwater trawls during 1977 rockfish survey and 1976 pilot survey.

	Position at beginning of tow		Depth (m)		
Date	Lat. (N)	Long. (W)	Gear	Bottom	Catch (kg)
		Bottom trawls			
8-15-76	36°42′	121°58′	101	101	459
8-19-76	36°20′	122°3′	212	212	627
8-19-76	36°30′	122°0′	177	177	4,120
7-18-77	35°33′	121°12′	132	132	519
7-27-77	36°59′	122°22′	124	124	4,722
7-27-77	37°10′	122°43′	176	176	881
7-30-77	37°19′	122°50′	144	144	2,790
7-30-77	37°18′	122°53′	240	240	2,499
8-4-77	38°21′	123°25′	144	144	954
		Midwater trawls			
8-12-76	36°56′	122°20′	154	229	3,314
8-13-76	37°11′	123°48′	302	302	3,156
8-13-76	37°12′	122°50′	282	285	1,415
8-19-76	36°18′	122°3′	161	165	3,313
8-20-76	36°27′	122°0′	274	274	7,264
7-27-77	37°13′	122°48′	245	247	4,055
7-27-77	37°21′	122°52′	188	192	3,578

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[3] Gunderson, D., and M. Nelson. 1977. Preliminary report on an experimental rockfish survey conducted off Monterey, California, and in Queen Charlotte Sound, British Columbia, during August-September 1976. Unpubl. manuscr., 82 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

midwater trawling was directed at concentrations detected through echo sounding.

Aimed midwater trawling could prove to be an efficient method of harvesting shortbelly rockfish which form large, off-bottom schools which are readily detected by echo sounding. The survey work indicated that with relatively little experience fishermen could learn to distinguish shortbelly rockfish from other abundant schooling species such as Pacific whiting which is the species most likely to contribute to unwanted by-catches.

Because of the small size of shortbelly rockfish, trawls would have to be constructed of mesh size smaller than allowed for bottom trawls by California regulations, 4.5 inches (11.43 cm). Cod ends used in the rockfish survey were constructed of 1.25-inch (3.18 cm) webbing. Mesh size experiments are required to determine optimum size for shortbelly rockfish.

The present California regulations are designed to prevent capture of flatfish and other rockfish that are smaller than desired. Thus by-catches of other fish should be considered. In the belief that fishermen targeting on shortbelly rockfish would limit their effort to areas producing large catches of shortbelly rockfish, catch compositions of hauls that produced more than 450 kg of shortbelly rockfish were compiled for bottom and midwater trawls made during the rockfish and pilot surveys.

The catch by weight of species other than shortbelly rockfish was considerably higher for bottom trawling (23.67 percent) than for midwater trawling (3.04 percent). Most of the by-catch was Pacific whiting for midwater trawling, while the by-catch for bottom trawling was dominated by chilipepper; bocaccio; Pacific whiting; jack mackerel, *Trachurus symmetricus*; and spiny dogfish, *Squalus acanthias*. Only 0.54 percent of the midwater trawl catches were composed of target species of domestic fishermen: Chilipepper, bocaccio, and sablefish. A relatively high 10.39 percent of the bottom trawl catches were composed of target species: Chilipepper; bocaccio; darkblotched rockfish, *S. crameri*, Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and jack mackerel.

The by-catch in a shortbelly rockfish fishery evidently can be kept at low levels by using only midwater trawls, but it would also be desirable to control age at recruitment. If mesh size restrictions prove impractical in accomplishing this, the relationships between size and age composition with depth and area of bottom trawl hauls indicated that fishermen may be able to minimize catches of relatively small or young shortbelly rockfish by choice of depth and area fished (Fig. 3, 4). Similar relationships are apparent between depth of haul and length compositions of large catches of shortbelly rockfish made by midwater trawls. Five out of nine large catches were made at depths exceeding 182 m (99.5 fathoms), and fish smaller than 200 mm fork length were not caught in significant numbers at these depths. Thus it appears that, at least during summer, fishermen may be able to minimize catches of small shortbelly rockfish through choice of depth fished. If mesh size restrictions prove practical, it appears that catches would be maximized by fishing at relatively deep depths.

Potential for Development of the Fishery

S. Kato, a fishery biologist specializing in fisheries development at the Tiburon Laboratory of the NMFS Southwest Fisheries Center, has identified several potential markets for shortbelly rockfish. There may be a small export market for good quality whole frozen fish. Another possible use is canning for either pet or human consumption, and a small test pack found the product acceptable as pet food. A possibly very large market exists for use as a raw product for surimi. The flesh appears to be of suitable quality for surimi, but their small size may make shortbelly rockfish more expensive to process than species currently used. Kato has tentatively estimated that the price to fishermen would be about $100 to $200 per ton. Actual prices, of course, will depend on a number of economic factors that can only be evaluated by fishermen and processors, and negotiations between the two parties.

High catch rates are necessary to support a fishery for a species that has a price range between $100 and $200 per ton. It would probably be necessary for a vessel to capture 10 to 20 tons per day to exceed operating costs. In addition to operating costs, capital outlays would be necessary to equip bottom trawlers for midwater trawling.

While the potential market, large biomass, and large catches shown in Table 1 indicated that there is considerable potential for development of a fishery for shortbelly rockfish. assistance by government agencies may be necessary for fullfillment of the potential. Kato has begun the development process by locating potential markets, purchasing appropriate fishing gear, and working with fishermen and processors in initiating a test fishery.

Management Options For Fishery Development

Management (State of California, Pacific Fishery Management Council, and U.S. Department of Commerce) has the option of either allowing or not allowing a fishery for shortbelly rockfish to develop. An argument against development of a fishery is that shortbelly rockfish have been shown to be prey items for important species such as chinook salmon (Merkel, 1957). On the other hand, Merkel's study showed that while shortbelly rockfish composed about 16 percent of the food of chinook salmon, 51 percent of the food was composed of northern anchovy, *Engraulis mordax*, Pacific herring, *Clupea harengus pallasi*, and squid (mostly *Loligo opalescens*). Significant fisheries have existed on these species without any documented evidence of causing feeding problems for chinook salmon. In addition Merkel estimated that euphausids composed 15 percent of the food of chinook salmon. Since shortbelly rockfish mainly feed on euphausids (Phillips, 1964), they may compete with chinook salmon.

Management also has the option of placing restrictions on types of gear, seasons, and locations. The results of this study suggest that it may be advisable to allow the use of midwater trawls but not bottom trawls because of relatively large by-catches of species other than shortbelly rockfish when bottom trawls are used. While yield per recruit and population fecundity analyses indicated that age at recruitment should probably be 3 or 4 years if a significant fishery develops, information is not available to make specific recommendations on obtaining that age at recruitment. The data (available only for summer months) indicated that fishermen may be able to avoid capture of small fish by choice of fishing depths and locations. No data are available on the practicality of using mesh size restrictions as a means to obtain a desired size at recruitment. Mesh size experiments and test fishing are required to determine the correct policy for obtaining a specific size at recruitment.

Estimates of a large biomass of shortbelly rockfish (295,000 t in a small portion of its range) indicated that the population could support a large fishery. However, the relatively low fecundity of the species suggests that caution in developing the fishery would be prudent. A relatively small fishery, e.g., 5,000-10,000 t of fish, may be desirable until more is known about the species. A small test fishery would allow development of procedures to obtain desired size at recruitment through mesh size experiments and monitoring of size and age composition of the catch with respect to depth and area of catch. Location and extent of areas containing high densities of fish would provide more information on size of the stock(s). Further analyses of larval survey data may provide additional estimates of stock size. Hydroacoustic midwater trawl surveys probably could be designed to produce estimates of stock size in areas of high densities of the species at relatively low cost. If the above data indicate the possibility of more than one important stock, appropriate studies should be carried out to determine the stock structure. Finally, additional work, such as predator-prey studies, on the position of shortbelly rockfish in the community is desirable. Ideally, management should take into account the effect of fishing on shortbelly rockfish on both its predators and competitors. However, as is the case for other marine fisheries, little is known on the interactions of shortbelly rockfish with other species.

Acknowledgments

Much of the data used for this report was collected by the 1977 rockfish survey and the 1976 pilot survey. The efforts of the skippers, crews, and scientific parties of the vessels *John N. Cobb, Commando, Miller Freeman, David Starr Jordan, Pat San Marie,* and *Pacific Raider* are appreciated.

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SOME STATISTICAL CONSIDERATIONS OF THE DESIGN OF TRAWL SURVEYS FOR ROCKFISH (SCORPAENIDAE)

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ABSTRACT

This study is in two parts. The first part reviews statistical theory for choosing among random, stratified random, and systematic sample survey schemes when strata are of equal size and receive equal sampling effort. The theory is applied to data collected during a pilot trawl survey for rockfish in Queen Charlotte Sound, British Columbia, and a full scale survey along the coasts of Washington, Oregon, and California. The results indicate that on a scale of about 80 km, a systematic survey scheme provides more precise estimates than the other schemes. However, the differences in precision are slight and probably should not outweigh other factors such as logistical constraints in the design of trawl surveys. The second part of the study reviews statistical theory for sampling from negative binomial distributions. Results of the Queen Charlotte Sound pilot survey indicate that except for fish with very low densities, numerous tows of short distances are relatively more precise than fewer tows of longer distances for trawl surveys for rockfish.

The Fisheries Conservation and Management Act of 1976 requires the development of fishery management plans for each marine fishery under jurisdiction of the United States. The requirement emphasizes the need to assess the status of U.S. fisheries. Estimates of stock abundance are essential for fishery assessment, and trawl surveys often are used to estimate absolute or relative stock abundance where suitable data from a fishery itself are lacking.

Very little data are available from the complex fisheries for rockfish (genus *Sebastes*) of the Pacific coast of North America. The fisheries are complex because many species and types of gear are involved. Often landing statistics do not specify species, and catches are seldom sufficiently sampled for age, length, and sex composition. Catch per effort data also are not reported by species and are difficult to interpret because of temporal changes in fishing power and target species.

Because of this lack of needed data, the Northwest and Alaska Fisheries Center of the National Marine Fisheries Service initiated a large scale trawl survey of rockfish stocks from southern California to the Aleutian Islands. The first stage of the 4-yr survey was to conduct pilot surveys in the Monterey Bay area, Calif., and Queen Charlotte Sound, British Columbia, during 1976. The overall goal of the pilot surveys was to provide information for design of the full scale survey. Gunderson and Nelson[2] describe the pilot survey and present preliminary results of the effort. A full scale survey was conducted in 1977 off the coasts of Washington, Oregon, and California. Design of the 1977 survey was partly based on results of the pilot surveys. Gunderson and Sample (1980) discussed the 1977 survey.

While trawl surveys have proven to be a useful tool for assessing fish stocks, problems still remain in their design and analysis. This paper presents analyses of results of the Queen Charlotte Sound pilot survey and 1977 survey. The analyses were aimed at answering three questions: 1) Should the full scale survey design be based on a random, stratified random, or systematic scheme? 2) Do results of the 1977 survey indicate that aspects of the design based on the pilot survey were correct? 3) What are the trade offs in precision between distance trawled and number of tows? Ancillary to question one are the questions: 1) Are there significant benefits to be gained by choosing one or a combination of the three sampling schemes? 2) Are there significant biases in estimates of

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[2] Gunderson, D. R., and M. O. Nelson. 1977. Preliminary report on an experimental rockfish survey conducted off Monterey, California and in Queen Charlotte Sound, British Columbia during August-September, 1976. Prepared for February 15-16, 1977 Interagency Rockfish Survey Coordinating Committee Meeting, Northwest and Alaska Fisheries Center, Seattle, Wash., 82 p.

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either means or variances using one or a combination of the three sampling schemes?

While our analyses are limited to data from the Queen Charlotte Sound pilot survey and the 1977 survey, the questions repeatedly arise in discussions of trawl surveys and thus are of general interest.

COMPARISONS OF RANDOM, STRATIFIED RANDOM, AND SYSTEMATIC SAMPLING

Methodology

Chapter 8 of Cochran (1964) discusses systematic sampling and presents methodology for choosing among random, stratified random, and systematic (every kth) sampling. Similar discussions are found in other sampling texts such as Hansen et al. (1953) and Sukhatme and Sukhatme (1970). The methodology used in comparing the three sampling techniques assumes equal sampling effort in each strata. If prior information indicated that variance differs considerably among strata, the optimal stratified random sampling scheme would not be equal allocation of sampling effort among strata. Unfortunately as shown by Abramson (1968), it can be difficult to obtain meaningful information on within strata variance for trawl surveys even if previous surveys have been made in the area. The methodology also only considers regularly spaced strata of uniform size. While prior knowledge (catch records) made it possible to design strata of unequal size on a large scale basis, knowledge is insufficient to do so on the scale considered in the analysis. The multispecies aspects of the survey made it particularly difficult to devise an optimal stratified random scheme.

In this section we use Cochran's notation. However, instead of examining components of variance for choosing among the three types of sampling as Cochran did, we calculated the variances for each type of sampling. Using the notation of Cochran, let a population of k possible systematic samples be represented by

Member	*Systematic sample number*				
	1	…	i	…	k
1	y_{11}	…	y_{i1}	…	y_{k1}
.	.		.		.
.	.		.		.
.	.		.		.
j	y_{1j}	…	y_{ij}	…	y_{kj}
.	.		.		.
.	.		.		.
.	.		.		.
n	y_{1n}	…	y_{in}	…	y_{kn}

where y_{ij} is the jth member of the ith systematic sample.

If the y_{ij}'s are arranged as they actually occur for a population of two systematic samples ($k = 2$) with four ($n = 4$) members they appear as follows:

Unit	1	2	3	4	5	6	7	8
Variable	y_{11}	y_{21}	y_{12}	y_{22}	y_{13}	y_{23}	y_{14}	y_{24}.

In a systematic survey a number (i) is chosen between 1 and k and then n members that are k units apart are sampled. Under a scheme of drawing one systematic sample, either units 1, 3, 5, and 7 or 2, 4, 6, and 8 would be observed. Under a stratified random scheme one unit out of each of four strata (units 1 and 2, 3 and 4, 5 and 6, and 7 and 8) would be chosen at random for observation. Under the corresponding random scheme any four of the eight units would be chosen at random to be observed. The example population contains 2 possible systematic samples, 16 possible stratified random samples, and 70 possible random samples. While more than 20% of the possible random samples match with a stratified random sample, <3% match with a systematic sample. A systematic sample is much more structured or constrained than the other schemes. Population variances of the means of random, stratified random, and systematic sampling are calculated as follows:

$$V(\bar{y}_{\text{ran}}) = \frac{N-n}{N} \; S^2_{\text{ran}}/n \tag{1}$$

where $V(\bar{y}_{\text{ran}})$ = variance of the mean calculated from random sampling ($\bar{y}_{\text{ran}}$),

$$N = k \times n,$$

$$S^2_{\text{ran}} = \sum_{i=1}^{k} \sum_{j=1}^{n} (y_{ij} - \bar{y})^2 / N{-}1,$$

$$\bar{y} = \sum_{i=1}^{k} \sum_{j=1}^{n} y_{ij} / N,$$

$$V(\bar{y}_{st}) = \frac{(N-n)}{N} S_{st}^2/n \qquad (2)$$

where $V(\bar{y}_{st})$ = variance of the mean calculated from stratified random sampling ($\bar{y}_{st}$),

$$S_{st}^2 = \frac{1}{n(k-1)} \sum_{j=1}^{n} \sum_{i=1}^{k} (y_{ij} - \bar{y}_{.j})^2,$$

$$\bar{y}_{.j} = \sum_{i=1}^{k} y_{ij}/k, \text{ and}$$

$$V(\bar{y}_{sys}) = \frac{1}{k} \sum_{i=1}^{k} (\bar{y}_{i.} - \bar{y})^2 \qquad (3)$$

where $V(\bar{y}_{sys})$ = variance of the mean calculated from systematic sampling ($\bar{y}_{sys}$),

$$\bar{y}_{i.} = \sum_{j=1}^{n} y_{ij}/n.$$

If k systematic samples are taken from a population that is sufficiently large to ignore the finite population correction factor then the variance estimates become:

$$S^2(\bar{y}_{ran}) = S_{ran}^2/n \qquad (4)$$

where $S^2(\bar{y}_{ran})$ = estimate of $V(\bar{y}_{ran})$,

$$S_{ran}^2 = \sum_{i=1}^{k} \sum_{j=1}^{n} (y_{ij} - \bar{y})^2 / (nk-1),$$

$$\bar{y} = \sum_{i=1}^{k} \sum_{j=1}^{n} y_{ij}/kn,$$

$$S^2(\bar{y}_{st}) = S_{st}^2/n \qquad (5)$$

where $S^2(\bar{y}_{st})$ = estimate of $V(\bar{y}_{st})$,

$$S_{st}^2 = \frac{1}{n(k-1)} \sum_{j=1}^{n} \sum_{i=1}^{k} (y_{ij} - \bar{y}_{.j})^2,$$

$$y_{.j} = \sum_{i=1}^{k} y_{ij}/k, \text{ and}$$

$$S^2(\bar{y}_{sys}) = \frac{1}{k-1} \sum_{i=1}^{k} (\bar{y}_{i.} - y)^2 \qquad (6)$$

where $S^2(\bar{y}_{sys})$ = estimate of $V(\bar{y}_{sys})$,

$$\bar{y}_{i.} = \sum_{j=1}^{n} y_{ij}/n.$$

Results of Pilot Survey

In the case of the Queen Charlotte survey, two random starting points were chosen and then tows were made along four transects for each of the two systematic samples. The transects within a systematic sample were approximately 16.1 km (10 mi) apart and bottom topography dictated some deviations from the desired transects. Because preferred depths differ among species of rockfish (e.g., *Sebastes alutus* is relatively scarce in shallow waters, while *S. proriger* is relatively scarce in deep waters), attempts were made to distribute sampling effort among 18.3 m (10-fathom) depth intervals within the depth range of concern, 91.4 m (50 fathoms) and 292 m (160 fathoms). Examination of the data indicated that, to obtain reasonable sample sizes, observations should be divided into only three depth intervals: 91-145 m (79 fathoms), 146-181 m (80-99 fathoms), and >181 m.

The Queen Charlotte data were organized in two ways to examine the relative precision of the three sample schemes. We first arranged tows at depths >181 m into a hypothetical population of four systematic samples for each species. While the original sample design called for two systematic samples, the two random starting points resulted in all transects being about 8.1 km (5 mi) apart. Each systematic sample contains two members. Furthermore, each hypothetical population is composed of x_{is} = the average catch (kilograms) per 1.8 km (nautical mile) of species s of all tows taken >181 m in transect i of the Queen Charlotte survey. Under the preceding definition the hypothetical population of systematic samples of species s is

$$\begin{array}{ccccc} \textit{Member} & \multicolumn{4}{c}{\textit{Systematic sample}} \\ & 1 & 2 & 3 & 4 \\ 1 & y_{11}=X_{1s} & y_{21}=X_{2s} & y_{31}=X_{3s} & y_{41}=X_{4s} \\ 2 & y_{12}=X_{5s} & y_{22}=X_{6s} & y_{32}=X_{7s} & y_{42}=X_{8s}. \end{array}$$

In this case $k = 4$ and $n = 2$. The y_{ij}'s are averages of 1-5 tows (Table 1). The resulting estimates of variance apply only to these hypothetical populations and particular mixture of tows per average (y_{ij}). It was not possible to construct similar hypothetical populations for the other depth intervals because of missing cells.

Values of V ($\bar{y}_{\text{ran}}$), V ($\bar{y}_{\text{st}}$), and V ($\bar{y}_{\text{sys}}$) for the first hypothetical populations are shown in Table 2. Comparison of the precision of the three sampling methods indicates that systematic sampling would be the most precise (has lowest variance) scheme for 8 of the 15 species. Ties occurred for the other seven species. Assuming that each species represents an independent observation, the sign test indicated that systematic sampling gave better results than stratified random sampling and random sampling at the 1% level of significance, and that stratified random sampling did not give significantly better results than random sampling.

TABLE 1.—Number of tows taken during the Queen Charlotte survey by stratum, systematic sample, member, and group of hypothetical populations.

	First group of hypothetical populations Systematic sample			
Member	1	2	3	4
1	1	1	1	2
2	2	2	4	5

		Second group of hypothetical populations Systematic sample	
Depth (m)	Member	1	2
91-145	1	2	8
	2	6	2
146-181	1	6	5
	2	2	1
>181	1	2	3
	2	4	9

TABLE 2.—Variances of means of catch (per 1.8 km towed) from the first hypothetical populations of Queen Charlotte rockfish. Calculations are made under random, stratified random, and systematic sampling schemes.

	Variance		
Population	Random	Stratified random	Systematic
Sebastes alutus	6,595.069	5,791.227	3,312.254
S. flavidus	0.188	0.188	0.188
S. pinniger	0.003	0.003	0.003
S. paucispinis	0.766	0.734	0.620
S. brevispinis	6.601	6.431	6.273
S. elongatus	0.002	0.002	0.002
S. proriger	0.002	0.002	0.002
S. babcocki	225.734	238.282	191.356
S. crameri	0.107	0.083	0.060
S. zacentrus	73.723	74.613	71.624
S. diploproa	0.344	0.329	0.329
S. entomelas	0.117	0.117	0.117
S. reedi	74.625	74.625	74.625
S. aleutianus	0.246	0.266	0.163
S. helvomaculatus	0.056	0.057	0.054

Because of the uneven distribution of tows per transect, we organized the data in another fashion to determine if the relative precision of the three sampling schemes is affected by organization of the data.

We next grouped the data into three depth intervals: 91-145 m, 146-181 m, and >181 m. In order to avoid missing cells it was necessary to create hypothetical populations of only two systematic samples with two members. We did so as follows: X_{isd} = the average of catch (kilograms) per 1.8 km of species s in depth interval d of all tows in transects i and $i+1$. The hypothetical population of systematic samples of species s from depth interval d is

$$\begin{array}{ccc} \textit{Member} & & \\ \textit{(stratum)} & \multicolumn{2}{c}{\textit{Systematic sample}} \\ & 1 & 2 \\ 1 & y_{11}=X_{1 \text{ and } 2,\, s,\, d} & y_{21}=X_{3 \text{ and } 4,\, s,\, d} \\ 2 & y_{12}=X_{5 \text{ and } 6,\, s,\, d} & y_{22}=X_{7 \text{ and } 8,\, s,\, d}. \end{array}$$

In this case $k = 2$ and $n = 2$. The y_{ij}'s are averages of 1 to 9 tows (Table 1). The values of V ($\bar{y}_{\text{ran}}$), V ($\bar{y}_{\text{st}}$), and V ($\bar{y}_{\text{sys}}$) are shown in Table 3.

The results indicate that systematic sampling produces more precise estimates of rockfish densities than either random or stratified random sampling. However, the sign test revealed that systematic sampling is not significantly better than stratified random sampling and only better than random sampling at the 5% level of significance. Stratified random sampling was not significantly better than random sampling. While systematic sampling appears to be the most precise of the three survey design schemes, there were many cases in which two or more of the schemes would be equally precise. In many other cases little precision would be lost if either stratified random or random designs were chosen.

Results of 1977 Survey

The 1977 survey design included both stratified random and systematic sampling strategies. The coast was stratified into three types of areas: high density sampling, low density sampling, and no

TABLE 3.—Variances of means of catch (per 1.8 km towed) from second hypothetical populations of Queen Charlotte rockfish. Calculations are made under random, stratified random, and systematic sampling schemes.

		Variance		
Population	Depth interval (m)	Random	Stratified random	Systematic
Sebastes alutus	91-145	82.313	59.446	55.285
S. alutus	146-181	2,745.670	3,803.277	1,125.770
S. alutus	>181	1,892.520	1,270.058	2,502.014
S. flavidus	91-145	8.442	12.750	0.102
S. flavidus	146-181	0.259	0.193	0.160
S. flavidus	>181	0.063	0.063	0.063
S. pinniger	91-145	257.220	234.198	228.577
S. pinniger	146-181	0.507	0.759	0.400
S. pinniger	>181	0.001	0.001	0.001
S. paucispinis	91-145	2.657	3.987	1.503
S. paucispinis	146-181	1.560	0.287	0.402
S. paucispinis	>181	0.260	0.197	0.121
S. brevispinis	91-145	60.440	19.718	13.783
S. brevispinis	146-181	8.703	13.020	11.262
S. brevispinis	>181	2.328	2.194	3.464
S. elongatus	91-145	0.129	0.100	0.102
S. elongatus	146-181	0.327	0.317	0.345
S. elongatus	>181	0.001	0.001	0.001
S. proriger	91-145	1,019.197	686.814	657.281
S. proriger	146-181	5.152	5.560	6.494
S. proriger	>181	0.002	0.002	0.002
S. babcocki	91-145	2.090	1.584	1.169
S. babcocki	146-181	3.241	0.339	0.339
S. babcocki	>181	49.730	50.671	24.671
S. crameri	91-145	0.001	0.001	0.001
S. crameri	146-181	0.057	0.051	0.029
S. crameri	>181	0.061	0.037	0.074
S. zacentrus	91-145	0.006	0.006	0.006
S. zacentrus	146-181	0.220	0.217	0.217
S. zacentrus	>181	29.261	30.641	30.641
S. diploproa	91-145	0.000	0.000	0.000
S. diploproa	146-181	0.000	0.000	0.000
S. diploproa	>181	0.165	0.162	0.162
S. entomelas	91-145	0.006	0.006	0.006
S. entomelas	146-181	0.609	0.724	0.378
S. entomelas	>181	0.048	0.048	0.048
S. reedi	91-145	0.000	0.000	0.000
S. reedi	146-181	0.302	0.302	0.302
S. reedi	>181	30.710	30.710	30.710
S. aleutianus	91-145	0.000	0.000	0.000
S. aleutianus	146-181	0.002	0.002	0.002
S. aleutianus	>181	0.087	0.057	0.018
S. helvomaculatus	91-145	0.000	0.000	0.000
S. helvomaculatus	146-181	0.001	0.001	0.001
S. helvomaculatus	>181	0.022	0.024	0.020

sampling. Areas in which historical fisheries data indicated high abundances of important rockfish species were assigned high density sampling. In these areas, transects were set at 8.1 km (5-mi) intervals. The typical high density area used in the study was about 81 km (50 mi) long. Transects in other areas were set at 16.1 km (10-mi) intervals unless bottom topography precluded sampling. Each transect was divided into four 91 m (50-fathom) depth strata between 91 and 457 m (250 fathoms). Sampled depths were then chosen at random within each depth stratum of a transect. The number of samples within a depth stratum was proportional to the bottom area of that stratum.

The survey design was based on several factors. The large scale stratification along the coast was an attempt to make sampling proportional to expected densities of important rockfish. This was done with the knowledge that there often are positive correlations among means and variances of fish densities. Depths were randomly chosen because it was known that often within an area densities of many species of rockfish sometimes only occur over a narrow depth interval. Thus, unless depths were chosen at random, bias could occur. Sampling was proportional to bottom area, because bottom area is used to convert fish densities to abundance estimates. Systematic transects were taken to ensure adequate aerial coverage for one intended use of the data, because of logistics and the results of the pilot survey.

Four high density areas had sufficient sampling effort to be included in the study. Eight or more adjacent transects were sampled in one or more depth strata in each chosen area. Area 1 was between lat. 34°33′ and 35°19′ N, area 2: lat. 35°19′ and 35°59′ N, area 3: lat. 39°7′ and 39°53′ N, and area 4: lat. 44°59′ and 45°50′ N. If more than one sample was taken from a depth stratum of a transect, one sample was chosen at random for the study. As in the case of the first Queen Charlotte hypothetical populations, populations of four or five systematic samples of two members each were created from the data. The results again indicated that systematic samples were slightly more precise than either random or stratified random (Table 4). The sign test indicated that systematic sampling was more precise than random at the 1% level of significance and stratified random at the 10% level. Stratified random sampling was not significantly less precise than random.

The data were also arranged into two systematic samples with four or five members each. Systematic sampling was more precise than random at the 1% level of significance, but was not significantly more precise than stratified random (Table 5). Stratified random sampling was not significantly less precise than random sampling.

Discussion

The results of this study indicate that on a scale of about 80 km along the coast systematic sampling for rockfish is slightly more precise than random sampling or a stratified random scheme with regularly spaced strata of equal size and

TABLE 4.—Variances of means of catch (per 1.8 km towed) from hypothetical populations of rockfish that were constructed from 1977 survey data. Calculations are made under random, stratified random, and systematic sampling schemes. Hypothetical populations are composed of either four or five systematic samples with two members.

				Variance		
Population	Systematic samples	Area	Depth interval (m)	Random	Stratified random	Systematic
Sebastes alutus	4	4	183-273	6,276.924	6,232.073	5,426.781
S. alutus	4	4	366-457	46.552	49.621	51.403
S. flavidus	4	2	91-182	0.090	0.102	0.074
S. pinniger	4	1	91-182	8.420	6.604	6.604
S. pinniger	4	2	91-182	0.185	0.215	0.422
S. paucispinis	4	1	91-182	9,630.529	9,888.812	8,989.353
S. paucispinis	4	2	91-182	34.452	39.381	27.818
S. paucispinis	5	2	183-273	24.181	23.665	30.904
S. paucispinis	5	3	91-182	37.490	42.176	81.772
S. brevispinis	4	4	183-273	2.185	2.290	1.421
S. elongatus	4	1	91-182	3.651	3.930	3.039
S. elongatus	4	2	183-273	0.060	0.054	0.054
S. elongatus	5	3	91-182	3.062	2.994	2.994
S. elongatus	4	4	183-273	63.100	66.665	93.148
S. babcocki	4	2	183-273	3.974	3.434	3.434
S. babcocki	4	2	274-365	4.998	5.820	8.106
S. babcocki	4	3	366-457	0.789	0.469	0.469
S. babcocki	4	4	183-273	7.761	6.086	6.125
S. babcocki	4	4	366-457	90.164	85.971	85.971
S. crameri	4	2	274-365	32.481	27.882	26.134
S. crameri	5	2	366-457	3.516	3.200	3.200
S. crameri	4	4	183-273	1,903.722	1,948.233	1,741.187
S. crameri	4	4	366-457	0.230	0.251	0.110
S. zacentrus	4	4	183-273	15.078	12.492	12.492
S. diploproa	4	2	183-273	1,255.342	1,389.344	1,317.551
S. diploproa	4	2	274-365	2,861.498	3,304.897	5,275.483
S. diploproa	5	2	366-457	2,727.360	1,979.702	948.597
S. diploproa	4	3	366-457	159.021	68.670	91.114
S. diploproa	4	4	183-273	683.478	700.234	779.467
S. diploproa	4	4	366-457	1.827	1.966	1.216
S. entomelas	4	1	91-182	467.709	468.780	476.280
S. entomelas	4	2	91-182	1.012	1.001	0.981
S. entomelas	4	2	183-273	3.050	3.103	2.633
S. entomelas	5	3	91-182	0.376	0.423	0.846
S. entomelas	4	4	183-273	3.002	3.057	2.129
S. aleutianus	4	4	366-457	589.997	688.030	399.129
S. goodei	4	1	91-182	119.235	119.105	121.329
S. goodei	4	2	91-182	4,439.160	4,391.472	4,226.895
S. goodei	4	2	183-273	416.868	468.696	301.373
S. goodei	5	3	91-182	258.380	221.057	220.347
S. jordani	4	1	91-182	467.621	406.738	399.790
S. jordani	4	2	91-182	26,765.442	27,254.716	25,958.703
S. jordani	4	2	183-273	7.256	8.158	5.457
S. jordani	5	3	91-182	0.575	0.570	0.570
S. saxicola	4	1	91-182	11,033.375	8,981.548	8,450.645
S. saxicola	4	2	91-182	145.957	162.133	120.545
S. saxicola	4	2	183-273	11,177.436	11,261.334	11,301.092
S. saxicola	4	2	274-365	0.244	0.235	0.235
S. saxicola	5	2	366-457	0.104	0.066	0.057
S. saxicola	5	3	91-182	3,402.868	3,070.065	3,068.507
S. saxicola	4	3	366-457	3.106	3.304	2.843
S. saxicola	4	4	183-273	4.630	4.187	3.308
S. rufus	4	2	183-273	10.247	11.501	10.092
S. rufus	4	2	274-365	6.588	6.561	7.374
S. rufus	5	2	366-457	0.513	0.566	0.870
S. aurora	4	2	274-365	6.835	7.591	6.215
S. aurora	5	2	366-457	22.452	24.477	20.423
S. aurora	4	3	366-457	54.214	45.845	45.465
S. aurora	4	4	366-457	0.507	0.511	0.782
S. melanostomus	4	2	274-365	0.566	0.148	0.148
S. melanostomus	5	2	366-457	22.167	20.848	24.547
Average				1,398.584	1,369.394	1,314.689

observations. It was also noted that our present state of knowledge precludes more optimally designed stratified random schemes on the scale considered. It appears that the decision to space transects of the 1977 survey in a systematic fashion was correct. While the data do indicate that systematic sampling is more precise than stratified random, the differences are slight and

TABLE 5.—Variances of means of catch (per 1.8 km towed) from hypothetical populations of rockfish that were constructed from 1977 survey data. Calculations are made under random, stratified random, and systematic sampling schemes. Hypothetical populations are composed of two systematic samples with four or five members.

				Variance		
Population	Members	Area	Depth interval (m)	Random	Stratified random	Systematic
Sebastes alutus	4	4	183-273	1,569.231	1,576.140	3,193.380
S. alutus	4	4	366-457	15.517	5.162	3.195
S. flavidus	4	2	91-182	0.030	0.034	0.063
S. pinniger	4	1	91-182	2.807	3.261	6.439
S. pinniger	4	2	91-182	0.062	0.072	0.141
S. paucispinis	4	1	91-182	3,210.176	3,203.033	2,889.063
S. paucispinis	4	2	91-182	11.484	13.142	24.503
S. paucispinis	5	2	183-273	6.045	5.266	3.534
S. paucispinis	5	3	91-182	9.373	10.639	1.145
S. brevispinis	4	4	183-273	0.546	0.226	0.336
S. elongatus	4	1	91-182	1.217	1.436	2.441
S elongatus	4	2	183-273	0.015	0.016	0.026
S. elongatus	5	3	91-182	0.766	0.656	0.656
S. elongatus	4	4	183-273	15.775	17.090	11.696
S. babcocki	4	2	183-273	0.994	1.102	0.130
S. babcocki	4	2	274-365	1.666	0.909	0.063
S. babcocki	4	3	366-457	0.263	0.197	0.002
S. babcocki	4	4	183-273	30.055	31.103	38.440
S. babcocki	4	4	366-457	1.940	0.551	1.000
S. crameri	4	2	274-365	10.827	12.414	2.403
S. crameri	5	2	366-457	0.879	0.372	0.372
S. crameri	4	4	183-273	475.931	378.362	426.423
S. crameri	4	4	366-457	0.077	0.107	0.035
S. zacentrus	4	4	183-273	3.770	0.485	0.281
S. diploproa	4	2	183-273	313.836	243.015	367.489
S. diploproa	4	2	274-365	953.833	869.422	1,065.206
S. diploproa	5	2	366-457	681.840	375.130	53.290
S. diploproa	4	3	366-457	53.007	25.279	0.191
S. diploproa	4	4	183-273	170.870	178.211	122.324
S. diploproa	4	4	366-457	0.609	0.803	0.090
S. entomelas	4	1	91-182	155.903	156.260	158.760
S. entomelas	4	2	91-182	0.337	0.402	0.856
S. entomelas	4	2	183-273	0.763	0.275	0.723
S. entomelas	5	3	91-182	0.094	0.106	0.000
S. entomelas	4	4	183-273	0.751	0.849	0.250
S. aleutianus	4	4	366-457	196.666	199.264	398.003
S. goodei	4	1	91-182	39.745	38.155	35.106
S goodei	4	2	91-182	1,479.720	1,367.750	1,531.744
S. goodei	4	2	183-273	104.217	127.159	335.989
S. goodei	5	3	91-182	64.595	72.201	140.660
S. jordani	4	1	91-182	155.874	163.576	85.794
S. jordani	4	2	91-182	8,921.814	9,116.721	7,983.423
S. jordani	4	2	183-273	1.814	2.179	0.004
S. jordani	5	3	91-182	0.144	0.137	0.137
S. saxicola	4	1	91-182	3,677.792	335.847	431.081
S. saxicola	4	2	91-182	48.652	55.079	106.864
S. saxicola	4	2	183-273	2,794.359	3,362.293	3,068.052
S. saxicola	4	2	274-365	0.081	0.069	0.069
S. saxicola	5	2	366-457	0.026	0.007	0.000
S. saxicola	5	3	91-182	850.717	916.415	388.878
S. saxicola	4	3	366-457	1.035	1.101	0.640
S saxicola	4	4	183-273	1.158	1.285	2.789
S. rufus	4	2	183-273	2.562	1.899	2.161
S. rufus	4	2	274-365	2.196	2.447	3.331
S. rufus	5	2	366-457	0.128	0.144	0.000
S. aurora	4	2	274-365	2.278	2.502	0.902
S. aurora	5	2	366-457	5.613	2.157	1.988
S. aurora	4	3	366-457	18.071	12.091	14.440
S. aurora	4	4	366-457	0.169	0.045	0.051
S. melanostomus	4	2	274-365	0.189	0.008	0.004
S. melanostomus	5	2	366-457	5.542	4.153	3.686
Average				427.483	375.349	375.586

probably should not outweigh other factors such as logistical constraints in the design of trawl surveys.

The sign test used to test the significance of differences among sample designs assumed that values for each species were independent. To examine this assumption we calculated correlation coefficients for each species pair in each combination of depth and area. Only samples containing at least one occurrence of each species of a pair were included. The average of the absolute value of the correlation coefficient is

0.324. This indicates that the assumption of independence is reasonable.

Even though our results indicate that systematic sampling is slightly more precise for the type of survey studied, the consequence of using a systematic design when another design may be more appropriate should be considered.

We first examine the effects of using a systematic design when in actuality the data are randomly distributed. Under these conditions the expected value of S^2y_{st} of Equation (5) is equal to the expected value of S^2_{sys} of Equation (6) and is related to the expected value of $S^2\bar{y}_{ran}$ of Equation (4) as follows:

$$\mathrm{E}\,(S^2_{st}) = \frac{nk-1}{nk-n}\ \mathrm{E}\,(S^2_{ran}).$$

Thus, random sampling will produce the lowest variance and if total sampling effort (nk) is constant, the variance of systematic and stratified random sampling will decrease relative to random sampling as n decreases. All three design strategies will result in unbiased estimates of the mean.

If there is a linear trend in the data such as shown below

Transect	1	2	3	4	5	6	7	8
Value	1	1.5	2	2.5	3	3.5	4	4.5,

then as Cochran (1964:217) showed, stratified random sampling is the same or more precise than systematic sampling, which is the same or more precise than random. The discrepancies increase as n increases.

If there are cycles in the data with a periodicity equal to or a multiple of spacing of transects such as

Transect	1	2	3	4	5	6	7	8
Value	1	2	1	2	1	2	1	2,

then systematic sampling is less precise than stratified random sampling, which is less precise than random sampling. The discrepancies increase as n increases. In addition, a single systematic sample would result in a biased estimate of the mean.

Systematic sampling is equal to or more precise than stratified random sampling which is equal to or more precise than random sampling if a population in which a plot of correlations between pairs of transects against distance between transects is concave upward and greater than or equal to 0 (Cochran 1964). Since systematic sampling was the most precise in this study, bias due to periodicity in the data should not be a problem.

Often in practice, investigators use a systematic sampling scheme with only one sample and calculate the variance as if the scheme is random. If V $(\bar{y}_{sys})$ is $<$V $(\bar{y}_{ran})$, as it appears to be for rockfishes, the resulting confidence limits would be conservative. The choice between precision and estimation of V $(\bar{y}_{sys})$ would depend on the objectives of the survey and the difference between V $(\bar{y}_{ran})$ and V $(\bar{y}_{sys})$. If V $(\bar{y}_{sys})$ is $<$V $(\bar{y}_{ran})$ and total number of transects is constant, increasing the number of systematic samples (k) in order to estimate V $(\bar{y}_{sys})$ causes the sampling scheme to become more like a random scheme and results in a corresponding increase in V $(\bar{y}_{sys})$ relative to V $(\bar{y}_{ran})$ (compare average variances shown in Tables 4 and 5).

A review by Cochran (1964) of a small number of surveys of terrestrial populations also indicated that systematic sampling is more precise than stratified random. Although Cochran did not state so, it also appeared that systematic sampling would be more precise than random sampling.

Two studies were found in the literature on marine populations. Venrick (1978) found that on the average systematic samples of chlorophyll in the water column produced estimates of total chlorophyll that were closer to the true value than stratified random samples, but was not able to compare precision of estimates for a given water column because only one systematic sample was taken from each column. She expressed a preference for stratified random sampling, because there tended to be more temporal correlations of deviations of the estimated values from the true values for the systematic samples than for the stratified random samples. The deviations were usually $<5\%$ and the temporal correlations probably could have been eliminated if the starting points of the systematic samples were observed at random instead of being fixed at the surface as was done in her study. Fiedler (1978) examined the relative precision of random, systematic, and stratified systematic transect surveys of northern anchovy, *Engraulis mordax*, school groups. He found that random sampling was the least precise of the three schemes. He also found that stratified systematic sampling was more precise than systematic sampling when school groups were distributed in a highly nonrandom way. Systematic sampling was more precise than stratified systematic sampling when sampling density was high. In other cases there were no significant differences between systematic and stratified systematic sampling.

Fiedler based allocations of sampling effort among strata on results of previous sampling. His results, in conjunction with those of Abramson (1968) and Venrick (1978), indicate the difficulty of determining optimum allocation of sampling effort among strata in the marine environment. The frustration of scientists who have attempted to do so is aptly stated by Venrick: "Study A demonstrated the dependence of the success of a sampling design upon the interaction of that design with the structure of the population being sampled; thus, it would seem that intelligent application of knowledge about the sampled population should improve the design. It was, therefore, disconcerting to find that RSS every 20 m, RSS-1, consistently performed as successfully as did RSS-3 which was designed by a presumably experienced worker (the author) with total knowledge about the population to be sampled."

We hope that improved knowledge on the distributions of populations will eventually result in more efficient allocation of effort among strata of systematic or random sampling schemes in the marine environment. However, we point out that fishermen still have their failures in attempting to restrict their sampling effort to times and areas of high fish catches in spite of years of experience, sophisticated fish finding equipment—presumably flexible sampling plans—and at times recent information from their colleagues.

EXAMINATION OF TRADE OFFS BETWEEN TOW LENGTH AND NUMBER OF TOWS

The distance trawled is an important factor to consider in the design of trawl surveys. Considerations include distance needed to obtain sufficient specimens for biological samples; time required to set and retrieve a trawl, to cover the distance, and to move between trawl locations; and the relationship among precision, tow length, and number of tows.

In this section we first use a negative binomial model with varying element size to estimate the relationship among precision and tow length and number of tows. We next use this relationship and time factors to illustrate the relationship between logistically feasible tow lengths and precision.

Animals in nature are rarely randomly distributed. They usually show some degree of aggregation or contagion. When these populations are sampled, they lead to distributions which are markedly skewed and have a large proportion of zero elements. The negative binomial distribution is often assumed for such populations because of practical performance (Laubscher 1961; Pielou 1969) and theoretical basis (Taylor 1953; Patil and Stiteler 1974). The distribution can be used to provide an estimate of the relationship between sample element size and precision.

The negative binomial distribution often is used to describe observed distributions in both general ecological research (Pielou 1969; Poole 1974) and fisheries research (Taylor 1953; Moyle and Lound 1960; Lambou 1963; Roessler 1965; Clark 1974). The distribution is characterized by two parameters, m the mean number of units per sampling element, and k, an "index of aggregation" (Waters 1959). The value of k varies inversely with the degree of aggregation of the population. The variance of a mean drawn from a population which follows a negative binomial distribution (V_{nb}) is a function of the mean (m) and k,

$$V_{nb} = m + m^2/k.$$

As the degree of aggregation increases, k approaches 0 and when the empty elements are ignored, this distribution approaches Fisher's logarithmic series. As the degree of aggregation decreases, k will approach infinity and the distribution converges to the Poisson.

The negative binomial can be derived from five or more different models, which may be mutually contradictory (Anscombe 1950; Bliss and Fisher 1953). A commonly used procedure to derive the distribution is to assume that it arises from a cluster of objects in space where the clusters follow a Poisson distribution and the number of animals in a cluster are distributed according to Fisher's logarithmic series. Taylor (1953) derived a form of the negative binomial as a probability model specifically to describe the relative abundance of fish species in trawl catches.

The data used for this analysis come from the pilot survey made in Queen Charlotte Sound. Since the negative binomial distribution is a discrete function, catches are measured in numbers of fish instead of weight as in the preceding section.

Fitting data from a systematically designed survey to the negative binomial distribution is a common practice (Moyle and Lound 1960; Taft 1960; Roessler 1965; Clark 1974). Hairston et al. (1971) made one of the few studies of sampling design for measuring spatial pattern. They found that estimates based on a grid (systematic) pattern were superior to those made from sampling at random. The grid pattern correctly reflected the spatial patterns of 17 of 22 species, while random sampling with the same number of samples correctly reflected only 12 of 22 species.

The standard negative binomial model requires a constant element size. This leads to two problems. The first is that comparisons can only be made at one sampling element size. The second problem is the negative binomial model cannot be fit to data with variation in sample element size.

To specifically deal with these problems, Bissell (1970, 1972) derived a negative binomial model that can be used when sample element size is variable and/or to predict the distribution of events for element sizes which differ from those on which the observations were based. The probability of observing x_i events on the i element which has a size of w_i is

$$P(x_i/w_i) = \{k/(mw_i + k)\}^k \quad \{mw_i/(mw_i + k)\}^{x_i} \prod_{j=i}^{x_i} \{(k + j - 1)/j\} \qquad (7)$$

where m = mean value of x_i for element size of unit size
k = parameter representing the degree of aggregation (Note that k in this section has a different meaning than in the section on sampling schemes)
w_i = element size (distance towed).

TABLE 6.—Estimates of mean densities ($\bar{d}$) (in numbers per kilometer), k, standard errors, with chi-square goodness of fit tests for trawl catches made in all depths in the Queen Charlotte survey.

Species	Mean density	SE($\bar{d}$)	k	SE(k)	Chi-square probability
Sebastes alutus	75.368	18.466	0.334	0 055	N.S.
S. flavidus	0.648	0.028	2.608	0.803	$P \leq 0.01$
S. pinniger	1.564	0.287	0.398	0.071	N.S.
S. paucispinis	0.508	0.072	2.546	0.814	N.S.
S. brevispinis	2.446	0.426	0.528	0.098	N.S.
S. elongatus	0.519	0.070	3.393	1.253	$P \leq 0.01$
S. proriger	30.402	9.612	0.198	0.031	$P \leq 0.05$
S. babcocki	1.723	0.273	0.665	0.131	$P \leq 0.01$
S. crameri	0.509	0.070	3.233	1.008	$P \leq 0.01$
S. zacentrus	4.973	1.428	0.274	0.044	$P \leq 0.01$
S. diploproa	0.623	0.102	1.157	0.292	$P \leq 0.01$
S. entomelas	0.119	0.028	6.289	1.004	N.S.
S. reedi	1.867	0.412	0 390	0.069	$P \leq 0.01$
S aleutianus	0.205	0.037	6.550	1.215	N.S.
S. helvomaculatus	0.301	0.048	4.424	1.078	$P \leq 0.01$

Iterative maximum likelihood solutions (Bissell 1972) gave estimates of values of m, k, and their standard errors relative to the average distance towed. The values were converted to densities (d) with units of numbers per kilometer. Estimates of d, k, and chi-square goodness of fit tests are given in Table 6. These tests were made by calculating the probability of a given number of fish occurring in a trawl of a given length from the probability density function given by Bissell (1972). This probability was cumulated over all trawls and then compared with the observed value using a chi-square test. Values of k from trawls in all depths ranged from 0.2 to 0.6 for the most abundant species. The low values of k indicate that the more abundant species are highly aggregated. The estimates for k are close to the value of k (0.27) that we estimated for *S. marinus*, an abundant species of rockfish, from Georges Bank from data in the paper by Taylor (1953).

We next divided the trawls into three depth intervals: 91-145 m, 146-181 m, and >181 m.

Estimates of mean densities, k, and goodness of fit tests by depth strata are presented in Table 7. The chi-square tests show that the data combined over all depths are not well represented by the negative binomial model. However, when the data are divided up by depth strata, the agreement is quite good. When the data from low density and high density depth strata are combined, the resulting frequency distribution has too many zero elements and too many high abundance elements. This results in the high chi-square values from trawls at all depths. In comparing the results in Tables 6 and 7, it is obvious that depth stratification is important. The differences between densities of species among depth strata were tested at the 10% level of significance. Of 43 possible comparisons, 27 (or 63%) were significantly different. This can be tested against what would have occurred randomly as a binomial proportion (Hollander and Wolfe 1973). The proportion is significantly different than random (z = 6.77,

TABLE 7.—Estimates of mean densities ($\bar{d}$) (in numbers per kilometer), k, standard errors, with chi-square goodness of fit tests for trawl catches by depth strata in the Queen Charlotte survey.

Species	Depth strata (m)	Mean density	SE($\bar{d}$)	k	SE(k)	Chi-square probability
Sebastes alutus	91-145	7.119	3.098	0.290	0.080	N.S.
S. alutus	146-181	90.816	37.533	0.419	0.132	N.S.
S. alutus	>181	131.914	36.838	0.693	0.197	N.S.
S. flavidus	91-145	1.160	0.253	1.660	0.817	N.S.
S. flavidus	146-181	0.724	0.200	2.037	1.030	N.S.
S. flavidus	>181	0.051	0.003	4.900	1.231	(1)
S. pinniger	91-145	5.200	2.084	0.322	0.090	N.S.
S. pinniger	146-181	0.465	0.136	2.155	1.063	(1)
S. pinniger	>181	0.018	0.017	(2)	—	—
S. paucispinis	91-145	1.051	0.308	0.870	0.323	N.S.
S. paucispinis	146-181	0.262	0.088	2.494	0.944	N.S.
S. paucispinis	>181	0.196	0.064	3.580	1.077	N.S.
S. brevispinis	91-145	4.401	1.435	0.531	0.160	N.S.
S. brevispinis	146-181	3.027	0.993	0.652	0.232	N.S.
S. brevispinis	>181	1.145	0.354	0.679	0.231	$P \leq 0.05$
S. elongatus	91-145	0.426	0.106	2.623	1.130	N.S.
S. elongatus	146-181	1.023	0.326	0.857	0.353	N.S.
S. elongatus	>181	0.193	0.062	4.535	1.334	N.S.
S. proriger	91-145	81.620	64.163	0.090	0.022	N.S.
S. proriger	146-181	4.701	1.901	0.440	0.146	N.S.
S. proriger	>181	0.053	0.031	5.968	1.537	(1)
S. babcocki	91-145	0.220	0.068	3.108	0.956	N.S.
S. babcocki	146-181	1.426	0.446	1.274	0.627	N.S.
S. babcocki	>181	4.526	1.395	0.600	0.170	N.S.
S. crameri	91-145	0.017	0.016	(2)	—	—
S. crameri	146-181	0.916	0.280	1.042	0.476	$P \leq 0.01$
S. crameri	>181	0.673	0.146	2.549	1.168	N.S.
S. zacentrus	91-145	0.118	0.047	4.040	1.098	N.S.
S. zacentrus	146-181	1.065	0.363	0.622	0.239	N.S.
S. zacentrus	>181	12.991	6.382	0.229	0.061	N.S.
S. diploproa	91-145	0.000				
S. diploproa	146-181	0.000				
S. diploproa	>181	1.563	0.504	0.496	0.154	$P \leq 0.01$
S. entomelas	91-145	0.034	0.024	4.442	1.087	(1)
S. entomelas	146-181	0.202	0.073	3.306	1.105	$P \leq 0.05$
S. entomelas	>181	0.142	0.053	4.451	1.241	N.S.
S. reedi	91-145	0.000				
S. reedi	146-181	0.066	0.039	4.124	1.177	(1)
S. reedi	>181	5.445	2.332	0.302	0.084	$P \leq 0.01$
S. aleutianus	91-145	0.000				
S. aleutianus	146-181	0.087	0.040	(2)	—	—
S. aleutianus	>181	0.517	0.125	2.379	1.035	N.S.
S. helvomaculatus	91-145	0.000				
S. helvomaculatus	146-181	0.022	0.022	3.277	0.908	N.S.
S. helvomaculatus	>181	0.844	0.227	1.098	0.457	$P \leq 0.01$

[1] Insufficient nonzero elements to perform chi-square test.
[2] Randomly distributed, $k \rightarrow \infty$.

$P<0.01$). Although the rockfish species tended to be aggregated, the group covers a wide range of spatial patterns.

In sampling from a negative binomial distribution, the precision of a density estimate for any given population depends both on the properties of the population, its density (d) and degree of aggregation (k), and on the characteristics of sampling, sample size (n) and the sample element size (S) (tow length). By modifying the sample characteristics, one can modify the precision of estimates.

Taylor (1953) showed in his Appendix E that reducing sample element size (length of the trawl) was the optimal sampling strategy under the condition that the total sampling area remained constant. That is, if A = area of strata (which is constant over all strata, i.e., $A_1 = A_2 = A_3 \ldots$), a = area of the sampling element, and n = the number of samples taken in each stratum, then the value $(a/A)n$ is fixed. Therefore, by reducing the length of tow, there must be a corresponding increase in the number of tows. However, in the body of his paper, Taylor implies that it would be advantageous to reduce sample element size even with a constant number of samples. His argument is based on the relationship between the mean and variance for a negative binomial population ($\mathrm{V}_{\mathrm{nb}_1}$)

$$\mathrm{V}_{\mathrm{nb}_1} = m + m^2/k.$$

The argument is that as m is reduced by some factor $1/b$, then $\mathrm{V}_{\mathrm{nb}_2}$ would only be

$$\mathrm{V}_{\mathrm{nb}_2} = m/b + (m/b)^2/k.$$

While this argument is correct, it does not mean that the estimate of total numbers of fish over the entire strata is more precise with decreasing sample element size. The effect of reducing sample element size on the variance of the estimate of the total number of fish in a stratum under the condition of a fixed sample size is considered below. Using the definitions of A, a, n from above, then N = total possible number of samples in a stratum where the sample element size equals a (i.e., $N = A/a$). The variance of the total number of fish in a stratum from n samples of the standard element size (V_{t_1}) is

$$\mathrm{V}_{t_1} = \frac{N_1^2}{n}\,\mathrm{V}_{\mathrm{nb}_1} \quad \text{or} \quad \mathrm{V}_{t_1} = \frac{A^2}{a^2 n}\left[m + \frac{m^2}{k}\right]$$

(Cochran 1964). The variance (V_{t_2}) of the total number of fish in a stratum for the sample element size reduced by $1/b$ is

$$\mathrm{V}_{t_2} = \frac{N_2^2}{n}\,\mathrm{V}_{\mathrm{nb}_2} = \frac{\left[\frac{A}{\left(\frac{a}{b}\right)}\right]^2}{n}\left[\frac{m}{b} + \frac{m^2}{b^2 k}\right]$$

$$= \frac{A^2 b^2}{a^2 n}\left[\frac{m}{b} + \frac{m^2}{b^2 k}\right] = \frac{A^2}{a^2 n}\left[bm + \frac{m^2}{k}\right].$$

The difference in variance between the different sample element sizes is

$$\mathrm{V}_d = \mathrm{V}_{t_2} - \mathrm{V}_{t_1}$$

$$= \frac{A^2}{a^2 n}\left[bm + \frac{m^2}{k}\right] - \frac{A^2}{a^2 n}\left[m + \frac{m^2}{k}\right]$$

$$= \frac{A^2}{a^2 n}\left[m(b-1)\right]. \tag{8}$$

Although there is actually an increase in overall variance by reducing sample element size with a constant sample size, it will be relatively small compared with the overall variance when m is large in value and/or k small:

$$\text{relative increase} = \frac{\frac{A^2}{a^2 n}\left[m(b-1)\right]}{\frac{A^2}{a^2 n}\left[m\left(1 + \frac{m}{k}\right)\right]}$$

$$= \frac{b-1}{1 + \frac{m}{k}}.$$

The purpose of many surveys is to produce total biomass estimates. These total biomass estimates are made by expanding a density estimate (usually in the form of a catch per unit effort measure) (Gunderson and Sample 1980) by the total area (Cochran 1964). Since measurement of the area involved can be made with relatively little error compared with the density estimate, we ignore error in area measurements in the following discussion. The precision of an estimate will vary inversely to its standard error. An index of precision ($P_{\bar{d}}$) is:

$$P_{\bar{d}} = \bar{d}/\mathrm{SE}_{\bar{d}}. \tag{9}$$

This index is the inverse of the coefficient of variation and is used here because it varies directly rather than inversely with precision. The density of a population is equal to the mean of the negative binomial distribution divided by the sample element size (S):

$$\bar{d} = m/S \tag{10}$$

where m = the mean of a number of tows of sample element size (S),
S = a constant sample element size with no variance.

The variance of m is

$$\mathrm{V}_m = (m + m^2/k)/n. \tag{11}$$

Therefore the variance of the density estimate is

$$\mathrm{V}_{\bar{d}} = (m + m^2/k)/nS^2 \tag{12}$$

and from Equation (10)

$$V_{\bar{d}} = (\bar{d}S + (\bar{d}S)^2/k)/nS^2 \qquad (13)$$

or

$$V_{\bar{d}} = \frac{\bar{d}}{nS} + \frac{\bar{d}^2}{nK}. \qquad (14)$$

The standard error of the density is

$$SE_{\bar{d}} = (V_{\bar{d}})^{1/2} \qquad (15)$$

$$= \left(\frac{\bar{d}}{nS} + \frac{\bar{d}^2}{nK}\right)^{1/2} \qquad (16)$$

and the index of precision is

$$P_{\bar{d}} = (\bar{d})/(\bar{d}/nS + \bar{d}^2/nk)^{1/2}$$

$$= (1/\bar{d}nS + 1/nk)^{-1/2}. \qquad (17)$$

From Equation (17), the precision of a density estimate will decrease as the degree of aggregation increases (i.e., $k \rightarrow 0$). For the case when $k >> \bar{d}$, then the index approaches $(\bar{d}nS)^{1/2}$ and a unit increase in sample size and sample element size are of equal importance. In the case of $\bar{d}$ approximately equal to k then sample element size has almost no effect on precision. When $\bar{d} >> k$, which is often the case for species that support a commercial fishery, the index simplifies to

$$P_{\bar{d}} \rightarrow (nk)^{1/2}. \qquad (18)$$

In these cases, only sample size will affect precision.

More specific evaluation of sampling negative binomial populations can be made by considering the estimates of k for three rockfish species and Equation (17). Since the limiting factor in these surveys is usually ship time and not cost in a direct sense, the evaluation is in terms of the most efficient use of a ship day. The first two species were the two target species in the Queen Charlotte Sound survey: *S. alutus*, a high density, highly aggregated species, and *S. flavidus*, a low density, highly aggregated species. The third species was *S. aleutianus*, a low density more randomly distributed species in Queen Charlotte Sound.

The sampling plan in Queen Charlotte Sound was to perform trawls of 0.5 h on the bottom which covered an average of 2.80 km. The average number of trawls per working day was 4.3. The average working day was 13 h long. Assuming 0.5 h on the bottom per trawl and 4.3 trawls/d, then the average nontrawling time per haul is 2.05 h. The minimum nontrawling time per haul was 1.07 h. The current sampling plan calls for an average of about 5 trawls/d. Using the above times, four possible alternative strategies are: 1) 3 trawls/d with gear at depth for 2.1 h, 2) 4 trawls/d with gear at depth for 1.2 h, 3) 5 trawls/d with gear at depth for 0.5 h, or 4) 6 trawls/d with gear at depth for 0.3 h.

Using the four strategies, values for precision of estimate of density were calculated for *S. alutus*, *S. flavidus*, and *S. aleutianus* and are shown in Figures 1, 2, and 3. The results of this analysis follow directly from the result of the general analysis. When the density to k ratio increases above a critical level, precision is for all practical purposes unaffected by changes in density. For the more randomly distributed species (*S. aleutianus*) the critical ratio occurs at higher density. For more aggregated species (*S. alutus*, *S. flavidus*) sample size (n) is not as effective in increasing $P_{\bar{d}}$ in an absolute sense as in the less aggregated species. Also, since sample size and sample element size are inversely related and precision increases with increased sample size except at very low density, sample element size has little effect on precision for these species except at very low density. Even for the less aggregated species, sample element size has little effect on precision except at low densities.

For a fixed amount of sampling effort, the precision of an estimate from a negative binomial population is a result of the interaction of population factors, density ($\bar{d}$) and degree of aggregation (k); and sampling factors, sample size (n) and sample element size (S). Analysis of the results of the Queen Charlotte Sound survey shows that rockfish species have a wide range of possible combinations of population factors. The analysis of sampling strategies showed that the same sampling plan could have been used for all three species with no significant loss in precision. This is due to the highly aggregated nature of rockfish species. However, for other less aggregated species, such as flatfishes, there would have been a greater difference among sampling schemes. This emphasizes the importance of picking target species on

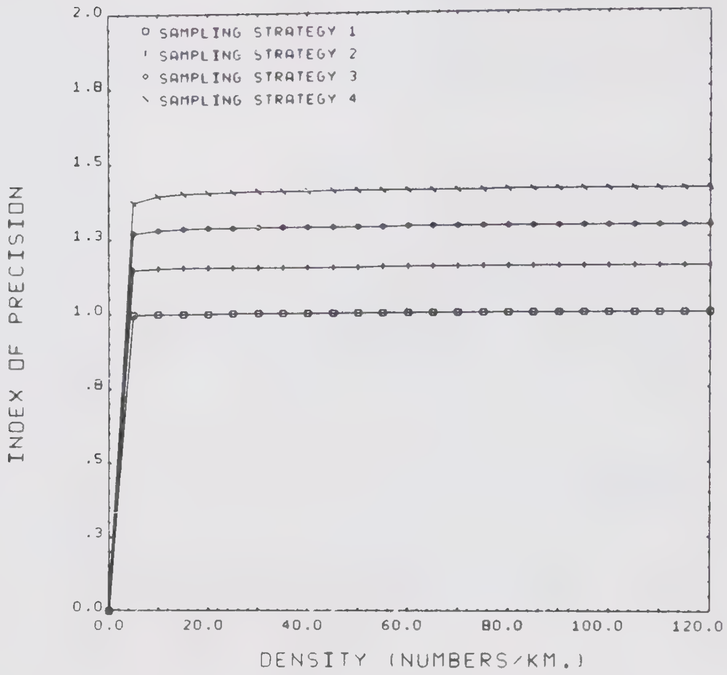

FIGURE 1.—Comparison of precision-density curves of four different sampling strategies for *Sebastes alutus*: 1) Three trawls/d with gear at depth for 2.1 h, 2) four trawls/d with gear at depth for 1.2 h, 3) five trawls/d with gear at depth for 0.5 h, and 4) six trawls/d with gear at depth for 0.3 h.

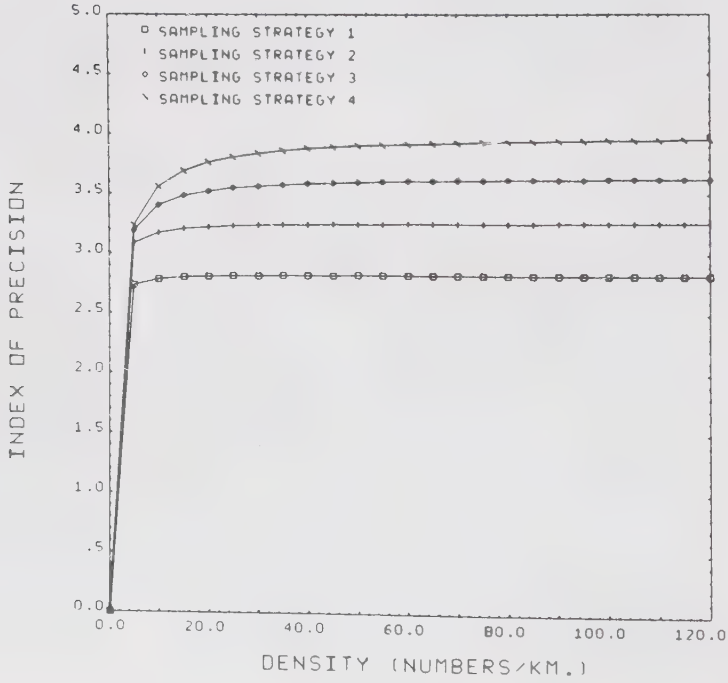

FIGURE 2.—Comparison of precision-density curves of four different sampling strategies for *Sebastes flavidus*: 1) Three trawls/d with gear at depth for 2.1 h, 2) four trawls/d with gear at depth for 1.2 h, 3) five trawls/d with gear at depth for 0.5 h, and 4) six trawls/d with gear at depth for 0.3 h.

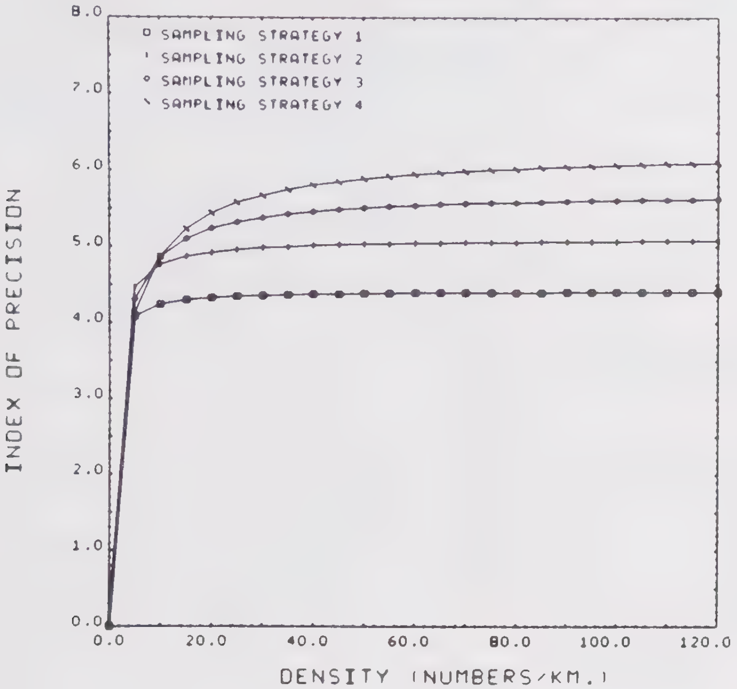

FIGURE 3.—Comparison of precision-density curves of four different sampling strategies for *Sebastes aleutianus*: 1) Three trawls/d with gear at depth for 2.1 h, 2) four trawls/d with gear at depth for 1.2 h, 3) five trawls/d with gear at depth for 0.5 h, and 4) six trawls/d with gear at depth for 0.3 h.

which to focus sampling strategies. For rockfish, these are likely to be high density, highly aggregated species. Generally, in sampling strategies for these species, the effects of sample element size would be unimportant. Increases in sample size would be much more important in terms of increased precision; however, increases in sample size would have to be fairly large to make a significant difference.

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POPULATION MODELS FOR THE NORTHERN ANCHOVY *(ENGRAULIS MORDAX)*[1]

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INTRODUCTION

The northern anchovy (*Engraulis mordax* Girard) is abundant off the coast of California and Baja California. The central subpopulation, or central stock, extends from 30°N to 38°N, and has been estimated at 3 to 4 million short tons' spawning biomass in recent years (Vrooman and Smith, 1972; Smith, 1972). The combined U.S. and Mexican harvests in 1977 were approximately 290000 short tons and show prospects for increase. The Mexican industry is unilaterally undertaking a major fishery expansion designed to provide domestic self-sufficiency in fish meal. This is estimated to require a 300000 to 500000 t harvest from the central stock. Simultaneously, the U.S. legislation which created the 200-mile fishery conservation zone requires all affected fisheries to be managed for "optimum yield". The resource will have to be allocated between U.S. and Mexican commercial fishermen, who wish to maximize their portions of the allowable catch, and the recreational fishermen, who wish to maintain the largest possible anchovy biomass to provide forage which will support large populations of predatory fish. Determination of optimum yield requires an analysis of the trade-offs between yield and stock size.

A surplus production curve would provide the basis for such an analysis, but no large fishery has previously exploited the resource in such a way that traditional fishery methods can be applied. However, the California Cooperative Oceanic Fishery Investigations (CalCOFI) program has conducted rigorous egg and larval surveys since 1950, providing an independent source of population size estimates. MacCall, Stauffer, and Troadec (1976) applied the Gulland potential yield formula (Gulland, 1970) to these biomass estimates, and concluded that the resource may have a potential yield of over 2 million t. An alternative to this crude and imprecise method is afforded by the time series of CalCOFI survey estimates itself (Fig. 1). The anchovy spawning biomass was remarkably small in the early 1950s, and grew over the following twenty years to an apparent equilibrium of nearly 4 million t. Since population growth at given initial size is a nearly direct measure of surplus production, the CalCOFI time series provides the makings of a surplus production model based on observed growth rates.

Before such a growth model can be constructed, we must examine the conditions under which that growth occurred. In particular, we must consider the reasons for the low biomass in 1951. A popular hypothesis has been that the decline of the California sardine (*Sardinops sagax caerulea*) left a void which the anchovy later filled. This hypothesis requires that the anchovy not be abundant before 1951 when the sardine biomass was large, and that sardine and anchovy abundances be negatively correlated. Results of recent work have been contrary to these assumptions. Soutar and Isaacs (1974) examined rates of scale deposition in anaerobic sediments off southern California for the past 150 years, and obtained a rank-correlation coefficient of +0·34 between sardine and anchovy scales. Assuming that scale deposition rates are proportional to population size, this strongly argues against an inverse relationship between population sizes. Further evidence is given by Smith (1972), showing that larval census estimates made from CalCOFI-like surveys in 1940 and 1941 indicate an anchovy spawning biomass of between 2 and 3 million t. At the same time, the sardine spawning biomass is estimated to have been 1·3 to 2 million t, so large populations of both species were existing simultaneously.

I offer an alternative hypothesis: the anchovy encountered a prolonged series of poor recruitments during the late 1940s, and the subsequent CalCOFI records document the recovery to more normal levels of abundance. While this hypothesis cannot be proved,

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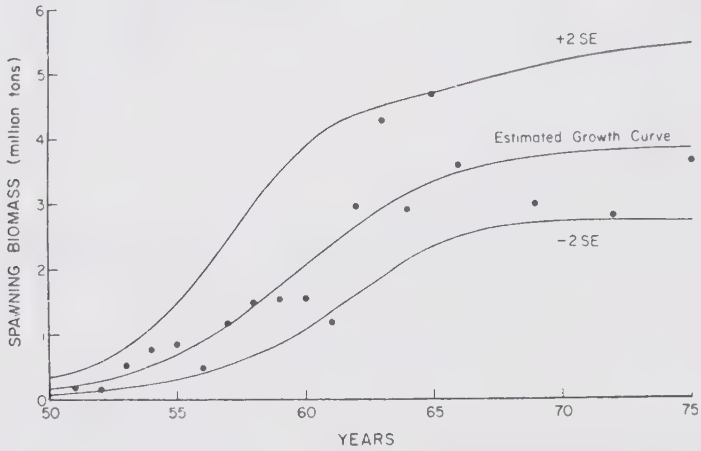

Figure 1. Historical increase in northern anchovy spawning biomass, with fitted growth curve and approximate confidence limits.

it is supported by two sets of evidence. The upwelling index of Bakun (1973) for 33°N 119°W (the Southern California Bight) in the second quarter of the year (April–June) shows a remarkable set of anomalies extending from 1947 to 1952 (Fig. 2). Upwelling during this period appears to have been much weaker than at any subsequent time. Lasker (1978) discusses some possible mechanisms for recruitment failure in the anchovy fishery. He indicates that insufficient upwelling in the spring may be a contributing factor, as the plankton blooms necessary for larval survival may not form in sufficient concentrations. If this actually occurred, we might expect to have seen poor recruitments in other pelagic species during the same period. Such was the case. The 1949 and 1950 year classes of the Pacific sardine were extremely weak, and contributed significantly to the final collapse of that fishery. The 1949, 1950, and 1951 year classes of Pacific mackerel (*Scomber japonicus*) were the smallest on record until the final collapse of that fishery in the 1960s (Parrish and MacCall, 1978). The Pacific bonito (*Sarda chiliensis lineolata*) virtually disappeared from southern California waters in the late 1940s until they returned in 1954 (Collins and MacCall, 1977). It appears reasonable that the northern anchovy, which shares the same environment, may have experienced similar recruitment difficulties.

In the following population growth model, I assume that events of the type described above are unusual. The sedimentary scale record of Soutar and Isaacs (1974) suggests that anchovy abundance was high and fairly constant from 1810 to 1925, but it appears to have been lower, and more variable, in recent years. The present model is based on conditions prevailing since 1951, and may therefore be optimistic. However, until adverse conditions occur, it is appropriate to base harvest rates on the current productivity of the resource. Safeguards can be incorporated into the resource management policy which will minimize the impact of unanticipated recruitment failures and rehabilitate the fishery at an optimal rate. Such a management policy will be described in a later section, after the population model is developed.

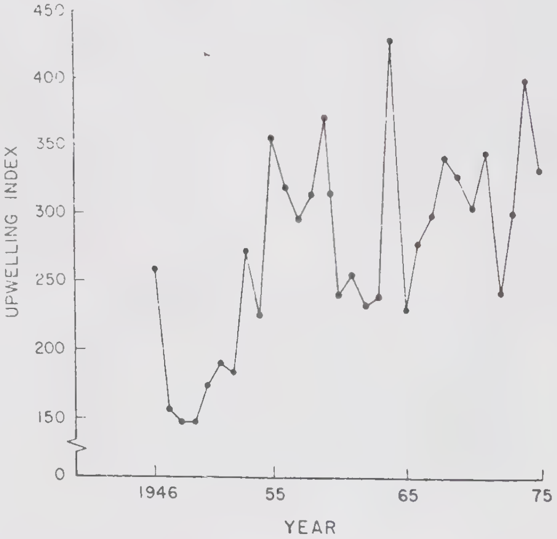

Figure 2. Mean upwelling index for April, May, and June, at 33°N 119°W (from Bakun, 1973).

DETERMINISTIC MODEL

The growth of the northern anchovy central subpopulation since 1951 followed a pattern empirically similar, if one allows for random variability, to the Verhulst-Pearl logistic growth curve. Many of the assumptions underlying the traditional logistic growth model cannot be met by the northern anchovy. However, it is quite reasonable as an empirical description of population growth, and has already been used in a variety of standard fishery production models. Whereas in those traditional models the nature of population growth is inferred from the response to fishery removals, the present model must infer the response to fishery removals, given a pattern of population growth. The basic components of the model are standard fishery equations, which were reassembled to describe annual population processes, and the effects of a fishery.

Spawning biomass is defined as the total weight of male and female fish in the population which have spawned at least once in their lives. In practice, only female fish, which produce detectable spawning products, are counted; males are assumed to be present in equal quantities. The spawning biomass is assumed to be proportional to the abundance of anchovy larvae (Smith, 1972). Since anchovy spawning usually reaches peak intensity in the spring, but can occur throughout the year, the annual census will be assumed to measure the spawning biomass on March 1 of each year. Recruitment is the addition of spawning biomass to the population by the entry of those individuals spawning for the first time. Recruitment is assumed to occur on the first birthday, since anchovies appear to spawn at age 1 (E. Knaggs, personal communication). Fish are assumed to become fully available to the fishery at the time they are recruited to the spawning biomass; however, they are partially available for the preceding few months.

The actual variation of spawning biomass throughout the year may look like the sinusoidal curve in Figure 3A. At "A", recruitment and somatic growth rates exceed the mortality rate so the population rapidly increases as new spawners enter the pool. At "B", the combined rates equal zero and the spawning population reaches peak biomass for the year. At "C", the recruitment rate has become very low so that mortality is the dominant force, causing the spawning biomass to fall until the next season's recruitment begins to enter the population. At "D", an autumn spawning is described, which would appear as a ripple in the main population cycle.

To be useful, a population model must simplify the events described above and relate them to quantities which we can measure. The model proposed here assumes that recruitment can be described as entering the spawning biomass *en masse* on March 1 of each year (Fig. 3B). The ichthyoplankton survey gives a spawning biomass estimate which is shown at "E". Subsequently, the cohort consisting of all spawners included in "E" declines in biomass owing to natural and fishing mortality, which is partially offset by somatic growth. "F" shows the remaining biomass at the end of the year which is augmented by the next recruitment (R) to give a new spawning biomass cohort at "G". "H" represents partial availability to the fishery before first spawning. The mathematical relationships between the biomasses at points "E", "F", and "G" are easily described by standard fishery equations.

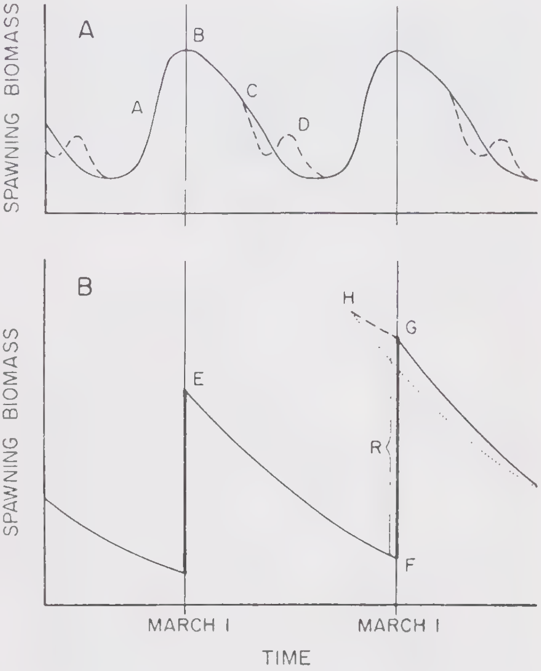

Figure 3. Diagrams of annual anchovy population processes: A, actual; B, model. Not drawn to scale.

The population at "F" is a function of the population at "E" and the combined rates of growth and fishing and natural mortality. If the rate of growth is expressed in similar fashion to rates of mortality, the equations become very straightforward. Letting G be the instantaneous or specific rate of growth:

$$G = \frac{dW}{W dt}$$

where W is fish weight. The combined instantaneous rate of loss of cohort biomass is $F+M-G$. In this analysis the quantity $M-G$ is used as an instantaneous rate of loss of biomass. Such an approximation must be used with caution, and should be discarded if better information is available. The survival of biomass (B) from March 1 (T) to time T+Δt is given by

$$B_{T+\Delta t} = B_T e^{-(F+M-G)(\Delta t)} \qquad (1$$

and the yield (Y) during the period is

$$Y = B_T \frac{F}{(F+M-G)}\left[1 - e^{-(F+M-G)(\Delta t)}\right]. \qquad (2$$

The biomass at "G" is the sum of the biomass at "F" and recruitment. In the absence of fishing, "E" and "G" are points on the logistic growth curve exactly 1 year apart. This relationship is described by

$$B^*_{T+1} = B_{T+1} + R_{T+1}$$
$$= \left[\frac{1}{B\infty} + \left(\frac{1}{B_T} - \frac{1}{B\infty}\right) e^{-r}\right]^{-1} \qquad (3)$$

where $B\infty$ is the asymptotic maximum biomass, r is the intrinsic rate of increase, and B^*_{T+1} represents a new cohort formed from the surviving biomass of the old cohort B_{T+1}, given by Equation (1), augmented by recruitment R_{T+1}. Recruitment is therefore given by (3) minus (1) where $F = 0$:

$$R_{T+1} = \left[\frac{1}{B\infty} + \left(\frac{1}{B_T} - \frac{1}{B\infty}\right) e^{-r}\right]^{-1} - B_T e^{-(M-G)}. \qquad (4$$

Thus the only independent variable in this spawner–recruit relationship is the spawning biomass 1 year prior to recruitment. In reality, the recruitment at time T+1 is provided by the previous year's spawning at time T, but also to some extent those at T–1 and possibly at T–2. Since the spawning biomasses at times T–1 and T–2 are relatively near that at time T, the error resulting from simplification to a 1-year cycle should be small.

The harvest of prespawners was included in the model to reflect more accurately actual fishery behavior. Fish were assumed to become partially available to the fishery (with φ as the coefficient of relative availability) for a length of time τ before spawning on March 1 (time T). The quantity (M-G) is assumed to be the same as that for spawners. The equivalent of fish alive at time T–τ would have been

$$R_{T+1-\tau} = R_{T+1} e^{(M-G)\tau} \qquad (5)$$

where R_{T+1} is as given in Equation (5) and $R_{T+1-\tau}$ denotes equivalent recruitment at that time earlier than March 1 when prespawners first become available to the fishery ("H" in Fig. 3B). Since fishing begins at time T+1–τ, the recruitment remaining at time T+1 (R^*_{T+1}) is

$$R^*_{T+1} = R_{T+1-\tau}\, e^{-(\varphi F+M-G)\tau}$$
$$= R_{T+1}\, e^{(M-G)\tau}\, e^{-(\varphi F+M-G)\tau}$$
$$= R_{T+1}\, e^{-\varphi F\tau} \qquad (6)$$

and the biomass at T+1 is

$$B^*_{T+1} = B_T e^{-(F+M-G)} + R_{T+1-\tau}\, e^{-(\varphi F+M-G)\tau} \qquad (7)$$
$$= B_T e^{-(F+M-G)} + R_{T+1}\, e^{-\varphi F\tau}. \qquad (8$$

The total yield of fish during the year is

$$Y = B_T \frac{F}{F+M-G}\left[1 - e^{-(F+M-G)}\right] + \omega R_{T+1}\, e^{(M-G)\tau}$$
$$\frac{\varphi F}{\varphi F+M-G}\left[1 - e^{-(\varphi F+M-G)\tau}\right] \qquad (9)$$

where ω is a coefficient of prespawner body weight in units of adult fish body weight.

Stochastic forms of the above model will be considered after the next section.

PARAMETER ESTIMATION

Two methods of estimating the logistic growth parameters, $B\infty$ and r, were used. First, approximate values were estimated by fitting the logistic growth equation to larval census estimates using a curvilinear least-squares regression procedure. This method requires us to ignore the effects that actual harvests may have had on the population growth, and therefore tends to bias the parameter estimates. An advantage of the method is that it gives approximate standard errors and covariances for the estimated parameters. The second estimation procedure was an iterative least-squares estimate using catch-corrected biomass estimates, in which the growth model was used to estimate yearly transitions. While providing better parameter estimates, this method does not provide estimates of standard errors, and requires the assumption that actual biomasses are equal to observed biomasses with respect to the impact of the fishery. Spawning biomasses (P. Smith, personal communication) and catches are given in Table 1, and parameter estimates are given in Tables 2 and 3.

Table 1. Catch, equivalent catch, and spawning biomass. Values in thousand short tons

	Total catch	Equivalent catch at year-end	Spawning biomass
1951	8·4	5·4	180
1952	42·7	26·9	156
1953	45·6	26·6	510
1954	28·5	17·4	768
1955	28·0	15·3	846
1956	36·3	21·1	485
1957	19·9	11·6	1 172
1958	9·5	6·0	1 479
1959	9·0	5·5	1 514
1960	7·6	4·5	1 540
1961	9·9	6·3	1 159
1962	8·8	5·5	2 985
1963	7·2	4·6	4 254
1964	12·7	8·0	2 901
1965	23·7	14·1	4 659
1966	66·4	40·7	3 572
1967	47·7	29·7	–
1968	40·6	27·5	–
1969	93·0	64·3	2 999
1970	107·9	78·7	–
1971	60·5	37·5	–
1972	59·1	40·9	2 784
1973	162·6	103·3	–
1974	142·9	95·7	–
1975	–	–	3 603

Table 2. Estimates of logistic growth parameters

Parameter	Curvilinear regression (no catches)	Iterative solution (corrected for catches)
B_∞ (GM)	$3{\cdot}611 \times 10^6$ t $36{\cdot}85 \times 10^{12}$ larvae	$3{\cdot}649 \times 10^6$ t
B_∞ (AM)	$3{\cdot}841 \times 10^6$ t $39{\cdot}19 \times 10^{12}$ larvae	$3{\cdot}888 \times 10^6$ t
r	0·3369	0·3638
A	3·231	3·195
$B(t = 0)$ (GM)	$137{\cdot}3 \times 10^3$ t $1{\cdot}401 \times 10^{12}$ larvae	$143{\cdot}6 \times 10^3$ t
$B(t = 0)$ (AM)	$146{\cdot}0 \times 10^3$ t $1{\cdot}490 \times 10^{12}$ larvae	$153{\cdot}1 \times 10^3$ t
RSS	1·976	2·035
GM to AM correction factor	1·0637	1·0657

Logistic parameters – first method

The logistic growth curve

$$B_t = \frac{B\infty}{1 + e^{-rt+A}} \tag{10}$$

where A is a constant relating to B_t at time $t = 0$ $[B(t = 0)]$, is a special case of the Richards growth curve (Richards, 1959; Pella and Tomlinson, 1969)

$$B_t = \left\{ B\infty^{1-m} + \left[B(t = 0)^{1-m} - B\infty^{1-m} \right] e^{-r(1-m)t} \right\}^{1/(1-m)} \tag{11}$$

where the skewness parameter (m) is equal to 2. Equations (10) and (11) are continuous equivalents to the annual transition Equation (3), but the former are more suited to regression because the independent variable, t, is not subject to large random error.

Regression also assumes that the residual variance is constant with respect to t, an assumption which is not met by the biomass data (Fig. 1). There may be several reasons for the increase in variance for the later years, including a change from monthly to quarterly cruises, and statistical properties associated with the increase in biomass itself. Much of the error in larval survey estimates arises from the clumped distribution of the spawning products. Taft (1960) showed the negative binomial distribution applied to such survey samples, with the characteristic that the variance increases rapidly with increases in the mean (abundance). Zweifel and Smith[2] (MS) give a preliminary estimate of CalCOFI larval survey sampling error based on the negative binomial distribution, in which a 95% confidence interval is described by a multiplicative factor of 1·2. Logarithmic transformation equalized the variance at high and low biomasses, supplying the condition of homoscedasticity necessary for proper regression estimates.

The parameters of the log transformations of Equations (10) and (11) were estimated by the curvilinear least-squares regression (Marquardt algorithm) given by Conway, Glass, and Wilcox (1970). Various values of m were tried, giving a minimum residual sum of squares (RSS) at approximately $m = 1{\cdot}6$ (Fig. 4). Since the RSS for $m = 2$ gives only a slightly higher RSS, the extra parameter in Equation (11) does not provide a statistically significant improvement in fit, and was therefore unnecessary. This justifies the use of the logistic growth curve in Equation (3) and simplifies estimation of the parameters.

Since the use of log-transformed variables results in the regression being fitted to the geometric mean of the raw data, a correction described by Beauchamp and Olson (1973) was applied to estimate the appropriate arithmetic mean. This correction consists of multiplying the antilog estimate of the mean by $e(s^2/2)$ where s^2 is the variance of the estimate $(RSS/n-3)$. In terms of the logistic growth Equation (10), the

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[2] James Zweifel and Paul E. Smith, NMFS, La Jolla, California, USA.

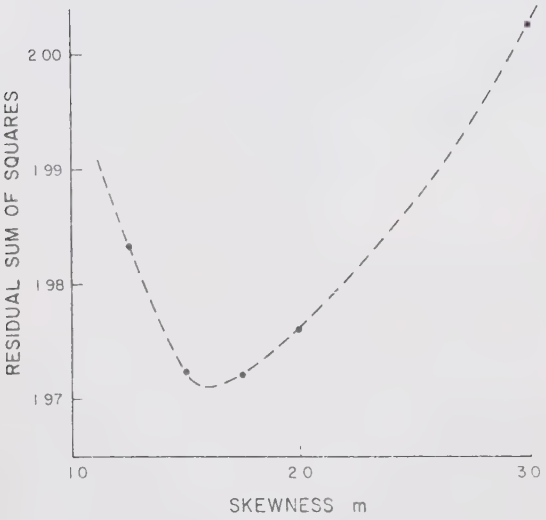

Figure 4. Minimum residual sums of squares as a function of the skewness parameter *m*.

correction is applied to $B\infty$. The parameter estimates are given in Table 2, and their standard errors and covariances are given in Table 3.

Approximate confidence limits for the growth curve (10) are obtained by the "delta method", which is basically a Taylor series approximation (Seber, 1973). In Seber's notation, the approximate variance of a function g which has parameters x_i, $(i = 1, 2, \ldots, n)$ is given by

$$V\left[g(x_1, x_2, \ldots)\right] = \sum_{i=1}^{n} V[x_i]\left(\frac{\delta g}{\delta x_i}\right)^2 + 2\sum_{ij} \operatorname{cov}[x_i, x_j]\left(\frac{\delta g}{\delta x_i}\right)\left(\frac{\delta g}{\delta x_j}\right) \qquad (12)$$

Since the log transform of Equation (10) was used in the regression, function g is the logarithm of (10), and the partial derivatives must be calculated appropriately. Also, $B\infty$ and its covariances do not yet incorporate the geometric mean correction factor, which in this case must be applied after taking antilogs of the estimated confidence limits. The approximate 95% confidence limits were calculated by the regression estimates ± 2 standard errors (Fig. 1).

Confidence limits for the rate of population growth are more interesting, as these have a direct bearing on the precision of the surplus production curve on which fishing strategy will be based. Annual growth rate is obtained by subtracting B_T from Equation (3), and approximate confidence limits were again calculated by the delta method. In this case the parameters used in the calculation were already corrected for the geometric mean. While the instantaneous growth rate function underlying the logistic growth curve is a symmetrical parabola, the corresponding annual growth rate (Fig. 5) as a function of initial biomass is skewed slightly to the right. The highest annual growth rate occurs at an initial biomass slightly smaller than $\frac{1}{2}B\infty$, such that the peak of the instantaneous growth rate curve is encompassed by the year's growth.

Logistic parameters – second method

The above estimates of logistic growth parameters were made under the assumption that actual harvest of anchovies during the period had negligible effect on population growth. Such an assumption was necessary in order to obtain parameter error estimates by the curvilinear regression procedure. The following parameter estimates for harvest-corrected growth incorporate a catch correction but do not have error estimates; errors are probably similar to those given previously (Table 3).

The second method employs the deterministic model (Equation 3) to give expected biomasses each year,

Table 3. Variance-covariance matrix for growth parameters estimated by curvilinear regression

			$B\infty$ 10¹² larvae *GM*	$B\infty$ 10¹² larvae *AM*	$B\infty$ 10³ t *GM*	$B\infty$ 10³ t *AM*	*r*	*A*
$B\infty$	(10¹² larvae)	*GM*	$(6{\cdot}513)^2$	–	–	–	–	–
		AM	–	$(6{\cdot}927)^2$	–	–	–	–
	(10³ t)	*GM*	–	–	$(638{\cdot}2)^2$	–	–	–
		AM	–	–	–	$(678{\cdot}9)^2$	–	–
r			– 221·6	– 235·7	– 21·71	– 23·10	$(0{\cdot}0560)^2$	–
A			546·8	581·6	53·6	57·0	0·00677	$(0{\cdot}271)^2$
			$n = 19$		$df = 19–3$		$t_0 = 1950$ A.D.	

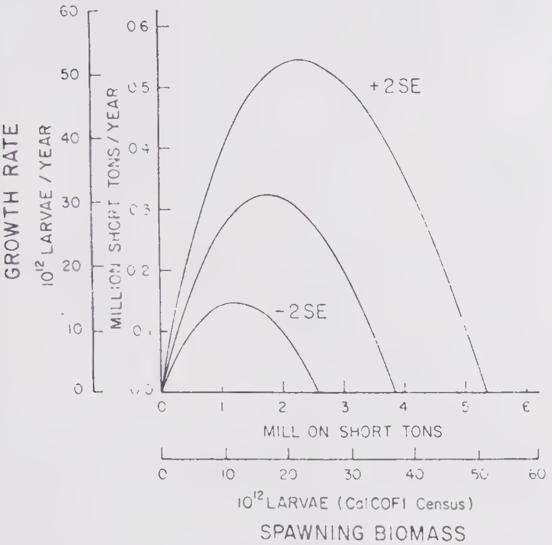

Figure 5. Logistic growth-rate curve and approximate confidence limits, with biomass measured alternatively in short tons or in CalCOFI larval census values.

allowing the time series to be fitted analogously to the first method. In order to correct for harvests, a quantity equal to the net year-end effect of the previous year's catch (Table 1) was subtracted from the expected population size. This quantity was determined by an application of cohort analysis. Equations (1) and (2) are analogues of the usual catch equations which employ only M and F. In this case, G is a constant instantaneous rate and can therefore be combined with F and M which are also constant instantaneous rates. Using the value of the specific growth rate constant developed in a later section, the quantity $(M-G) = 0{\cdot}8$ was substituted for M in the cohort analysis equations (Tomlinson, 1970) allowing cohort analysis of a population measured in weight rather than numbers.

Monthly catches in weight were compiled for a March-to-February year. California landings by month were obtained from the California Marine Fish Landings series of *Fish Bulletins* from the California Department of Fish and Game. Bait landings were also obtained from the above source, but only annual totals are given. The bait catch was arbitrarily divided equally among June, July, August, and September, the months of maximum bait harvest. Mexican catches were obtained from MacCall, Stauffer, and Troadec (1976), and from recent unpublished fishery reports. Since no data are available on Mexican catches before 1962, arbitrary values of 100 t in 1956 increasing by 100 t annually to 500 t in 1960 were used. Again, only annual totals are available, so the Mexican catches were divided into the same 4-month period as the bait catch. This division is consistent with the Ensenada-based fishery which operates mainly during the summer months.

A "forward solution" form of cohort analysis was used to find the surviving biomass of the spawners at the beginning of the next spawning season. An initial value of fishing mortality was obtained by solving Equation (2) for F, given the total March landings and the larval survey estimate of spawning biomass (March 1). Monthly biomasses were then estimated sequentially to give biomass on the following March 1. This final biomass was then subtracted from the biomass which would be indicated by Equation (1) had there been no fishing. This difference is the catch correction factor applied to biomasses predicted by Equation (3). It can be viewed as the catch which would have the same net effect as the true catches, had it been taken entirely on the last day of February. Annual catches and year-end equivalent catches are given in Table 1.

Parameter values were estimated by an iterative procedure based on searching the response surface for the minimum residual sum of squares (Stauffer, 1973). Three trial values of each of the parameters r, $B\infty$ and $B(t=0)$ were selected, giving 27 combinations in all. The 19 biomass estimates corresponding to the CalCOFI surveys from 1951 to 1975 were predicted by each combination of three trial parameter values, and a residual sum of squares (RSS) for the logarithm of the biomasses was calculated. A multiple linear regression program (BMD02R) was utilized to estimate coefficients of the following equation used to model the residual sum of squares response surface:

$$\begin{aligned} RSS = {} & b_0 + b_1\,B\infty + b_2 r + b_3\,B(t=0) + b_4\,B\infty^2 + b_5 r^2 \\ & + b_6\,B(t=0)^2 + b_7 r\,B\infty + b_8\,B\infty\,B(t=0) \\ & + b_9 r B(t=0). \end{aligned} \tag{13}$$

The values of r, $B\infty$, and $B(t=0)$ that minimize the RSS are the solution to the three first order partial derivatives of (13), with respect to r, $B\infty$, and $B(t=0)$, set equal to zero, i.e.,

$$\frac{\delta RSS}{\delta B\infty} = b_1 + 2b_4\,B\infty + b_7 r + b_8\,B(t=0) = 0$$

$$\frac{\delta RSS}{\delta r} = b_2 + 2b_5 r + b_7 B\infty + b_9\,B(t=0) = 0$$

$$\frac{\delta RSS}{\delta B(t=0)} = b_3 + 2b_6 B(t=0) + b_8\,B\infty + b_9 r = 0.$$

These can be rewritten in terms of matrix algebra as

$$Dx = d$$

where the matrix $D = \begin{bmatrix} 2b_4 & b_7 & b_8 \\ b_7 & 2b_5 & b_9 \\ b_8 & b_9 & 2b_6 \end{bmatrix}$

the vectors $x = \begin{bmatrix} B \\ r \\ B(t=0) \end{bmatrix}$ and $d = \begin{bmatrix} -b_1 \\ -b_2 \\ -b_3 \end{bmatrix}$

From this, the values of r, $B\infty$, and $B(t=0)$ that minimize RSS can be expressed as

$$x = D^{-1}\,d \tag{14}$$

Since Equation (13) only approximates the response surface, about four iterations of the above parameter estimation procedure with successively closer delineations of the trial parameter region gave results precise to three significant digits in most cases. An independent test of accuracy is furnished by the previous curvilinear regression estimates. An iterative solution was run for the case of "no catches", giving results very similar to the regression estimates. It is interesting to note that this solution, which includes the effect of actual harvests, gives a slightly larger minimum RSS than does the previous regression solution (Table 2). This suggests that the small fishery which has existed does not account for a detectable portion of the variance in biomass which has been observed.

Other parameters

The parameters M and G always appear in combination as $(M-G)$, which can be interpreted as instantaneous rate of natural decrease in biomass, and which were estimated as such by the following approximation (Table 4). Growth from age 2 to age 3 was considered typical of the population. Mean length at age (Spratt, 1975) was expanded by the length–weight relationship (Collins, 1969) to obtain approximate mean weight. Survival was assumed to be 1·0 at age 2, and 0·346 at age 3, based on $M = 1{\cdot}06$ (MacCall, 1974). The difference of the logarithm of approximate cohort biomasses was 0·75, and was rounded to 0·8 as a functional estimate of the quantity $(M-G)$.

Table 4. Approximation of $(M–G)$

Age	Mean length (mm-SL)	Weight (g)	Numbers in cohort	Weight of cohort	ln weight of cohort
2	112	14·2	1·000	14·25	9·55
3	124	19·3	0·346	6·69	8·81
				Difference =	0·75

Table 5. Mean weight data for estimation of ω and φ

Season	Ratio mean weight Age 0 to mean weight age 1+	Ratio catch Age 0 to catch age 1+
1965/1966	0·542	0·0254
1966/1967	0·501	0·0370
1967/1968	No data for southern California	
1968/1969	0·765	0·1740
1969/1970	0·636	0·2347
1970/1971	0·639	0·0270
1971/1972	0·639	0·0812
1972/1973	0·815	0·0852
1973/1974	0·642	0·0478
Mean	0·647	0·0890
Standard deviation	0·103	0·0764

The quantity ω is the ratio of the weight of an average prespawner (age 0) to that of an average spawner (age 1 and older). By dividing total weight landed by total number of fish landed for each category, average weights for these two groups were obtained from the landings reports. The average ratio of these average weights gives an estimate of $\omega = 0{\cdot}647$ (Table 5).

Prespawning anchovies are assumed to be partially (φ) available to the fishery for a short period (τ) before they spawn on their first birthday. Relative availability is defined as

$$\varphi = F_0/F_{1+} \tag{16}$$

for the same reason. Harvest of prespawners is given by

$$Y_0 = F_0\,\bar{B}_0\tau \tag{17}$$

where $\bar{B}_0$ is the average biomass of prespawners during the period of availability preceding spawning. Harvest of adult anchovies is given by

$$Y_{1+} = F_{1+}\,\bar{B}_{1+} \tag{18}$$

where time is unity, being one fishing year. Therefore, (17) and (18) are substituted into (16) to obtain

$$\varphi = (Y_0/Y_{1+})\,(\bar{B}_{1+}/\bar{B}_0\tau). \tag{19}$$

The quantity Y_0/Y_{1+} can be obtained from fishery data (Table 5), and the theoretical ratio of mean biomasses can be obtained from the model.

The mean biomass of adult fish is given by

$$\bar{B}_{1+} = \int_{t=0}^{\infty} B'\,e^{-(F+M-G)t}\,dt$$

$$= \frac{B'}{F+M-G} \tag{20}$$

where $t = 0$ denotes time of first spawning, and B' denotes the biomass at that time. This equation uses the approximation that the biomass of all adult cohorts in a single season is equivalent to the biomass of a single cohort over its lifetime. The mean biomass of prespawners during the period of partial availablity is

$$B_0 = \frac{1}{\tau} \int_{t=-\tau}^{t=0} \omega B' \, e^{-(\varphi F+M-G)t} \, dt$$

$$= \frac{\omega B' \, [e^{(\varphi F+M-G)\tau}] - 1}{\tau(\varphi F+M-G)} . \qquad (21)$$

Equations (20) and (21) are now substituted into (19) to obtain

$$\varphi = \frac{Y_0}{Y_{1+}} \cdot \frac{\varphi F+M-G}{\omega(F+M-G) \, [e^{(\varphi F+M-G)\tau} - 1]} . \qquad (22)$$

The quantity φ can now be estimated by iteration, given values of the remaining variables. The historical average value of Y_0/Y_{1+} has been 0·089 (Table 5). The fishing mortality rate F has averaged 0·03, and $(M-G)$ was estimated above to be 0·8. Age 0 anchovies first appear in January, about 0·2 years before spawning on March 1, so for $\tau = 0{\cdot}2$, φ is estimated to be 0·76.

DISCUSSION OF THE DETERMINISTIC MODEL

The deterministic model described above allows equilibrium yield to be described as a function of spawning biomass (Fig. 6). Equilibrium yield is defined as that yield which is expected to maintain the spawning biomass at the same level in the following year. Note that this is not equivalent to sustainable yield, because natural fluctuations in recruitment success will not allow a given biomass to be maintained. Sustainability decreases with increasing variability and will be discussed in more detail later.

A somewhat surprising result of the model is that the equilibrium yield is considerably greater than the expected population growth in the absence of a fishery (560000 t per year as opposed to 353000 t per year). This is contrary to the assumption of equality often made in production modeling, and arises from the fact that reproduction is periodic rather than continuous with immediate recruitment. Qualitatively, the phenomenon arises from the competing risk of death from fishing and natural causes, so that many fish taken by the fishery would not have reproduced at the next spawning in any case. A simple correction factor can easily be derived from guesses of mortality rates, and could significantly improve the performance of catch-transition production models (e.g., Schaefer, 1957; Pella and Tomlinson, 1969), particularly when applied to stocks in which reproduction is seasonal (MacCall, 1978).

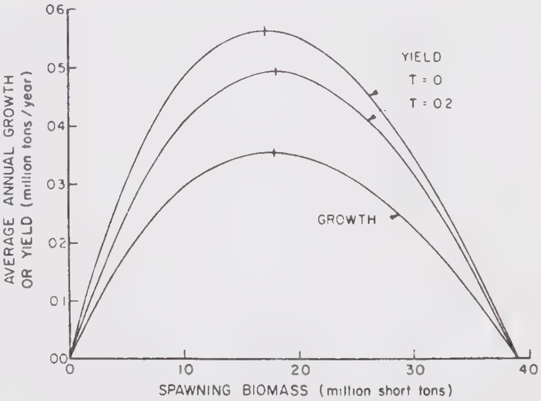

Figure 6. Equilibrium yield and growth rates for the northern anchovy central stock. Growth is mean population growth in the absence of fishing. Equilibrium yield is given for no harvest of prespawners ($\tau = 0$), and for partial availability of prespawners ($\tau = 0{\cdot}2$).

Another rather surprising property of the equilibrium yield curve is the fact that yield decreases when prespawners are harvested (484000 t per year as opposed to 560000 t per year). Yield per recruit considerations indicate that maximum yield per recruit is obtained by fishing the resource intensively with a small size at entry (MacCall, Stauffer, and Troadec, 1976). The present model, which includes reproduction, indicates that harvesting anchovies immediately before spawning results in a twofold loss to the population: loss of the fish and of its progeny. The model predicts that yield will generally be near a maximum when fish are taken as soon after spawning as possible. Whether these are valid conclusions remains to be seen. For comparison, the Peruvian anchoveta fishery was highly productive under intensive fishing of prespawners in the 1960s. However, the above two considerations may also help explain the unexpectedly slow recovery of the anchoveta resource since the population collapse of the early 1970s.

STOCHASTIC MODEL

While the above deterministic model is useful for estimating the approximate long-term productivity of the northern anchovy central stock, it is unable to provide a realistic and useful description of short-term productivity and variability. Spawning biomass has shown large fluctuations about the hypothesized trend (Fig. 1). A simple stochastic model can be derived from the second method (iterative least squares) of logistic parameter estimation described above. Equation (3) of the population growth model can be rewritten as

$$\ln B_T = \ln (B_T + R_T) = \ln\left[\frac{1}{B\infty} + \left(\frac{1}{B_{T-1}} - \frac{1}{B\infty}\right)e^{-r}\right]^{-1} + \varepsilon \quad (23)$$

or more simply

$$\ln B_T^* = \ln \hat{B}_T^* + \varepsilon$$

where ε is a stochastic error term with mean = 0, B_T^* is surviving biomass plus recruitment, and $\hat{B}_T^*$ is predicted from B_{T-1} by the deterministic growth model. There are three principal sources of this error: 1) variability of population processes, particularly recruitment, 2) error of observation of biomass at time T, and 3) error of observation at time T−1. A more complicated model could be constructed with stochastic errors in recruitment and in observed population size respectively. Such a model would allow simulations of population and fishery behavior over long periods. However, there is at present no definitive way to separate the components of the error term in (23). Thus there would be a wide spectrum of simulation model results depending on the portion of the variability assigned to recruitment.

The simple stochastic model (23) does not require that the error term be separated into components, but requires the assumption that the effect of the fishery on a population of the observed biomass would be a close approximation of the effects of a fishery on a population of the actual biomass. This assumption also occurs in the second method of logistic parameter estimation, so the parameters inherently reflect this assumption. On the other hand, there is a definite non-linearity in the model, such that responses to an underestimated biomass are not equal and opposite to responses to an equally overestimated biomass. This problem should not be severe except when large catches are being taken from small biomasses.

A plot of $\ln B_T^*$ against $\ln \hat{B}_T^*$ from 1952 to 1966, where the latter variate is corrected for catches according to the second logistic parameter estimation method, shows the deterministic model to be a good description of the average year-to-year behavior of the observed spawning biomasses (Fig. 7). The residual error term ($\varepsilon = \ln B_T^* - \ln \hat{B}_T^*$) is well behaved when plotted against $\ln \hat{B}_T^*$ (Fig. 7), with a mean of 0·016 and a standard deviation of 0·496. The mean is sufficiently near zero to justify acceptance of the parameter estimates of $B\infty$ (arithmetic mean) and r for predictive purposes. The residuals show no distinct changes in pattern over the range of observed biomasses. Therefore, ε will be assumed to be normally distributed ($\mu = 0$, $\sigma = 0{\cdot}496$) in the stochastic model.

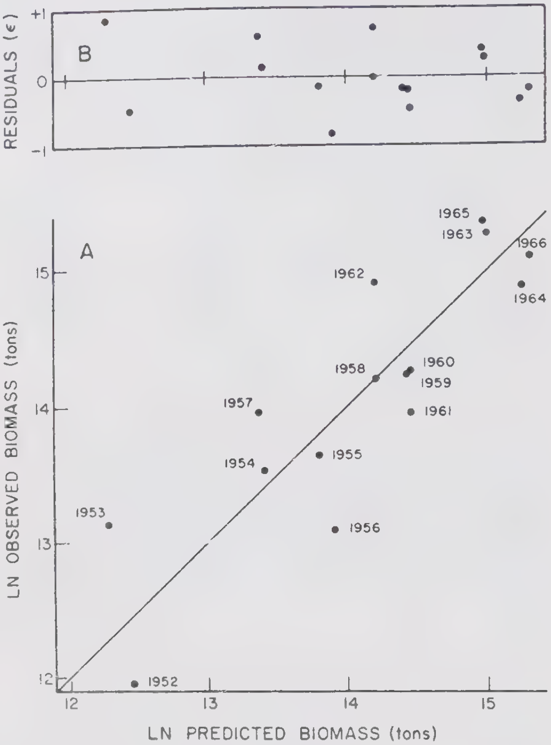

Figure 7. Comparison of predicted and observed spawning biomasses, including a plot of residuals.

Equation (23) is equivalent to

$$B_{T+1}^* = B_{T+1} + R_{T+1} = e^{\varepsilon}\left[\frac{1}{B\infty} + \left(\frac{1}{B_T} - \frac{1}{B\infty}\right)e^{-r}\right]^{-1} \quad (24)$$

so if there is no fishing, R_{T+1} can be obtained by the analogue of (4):

$$R_{T+1} = e^{\varepsilon}\left[\frac{1}{B\infty} + \left(\frac{1}{B_T} - \frac{1}{B\infty}\right)e^{-r}\right]^{-1} - B_T e^{-(M-G)} \quad (25)$$

Note that R_{T+1} is not actual recruitment, but apparent recruitment, since the observation error of B_T and B_{T+1} is included in the stochastic error term. For this reason, apparent recruitment can become negative for low values of e^{ε}. Equation (25) can be used to estimate

Table 6. Conditions for negative apparent recruitment, and probabilities of occurrence based on an assumed normal distribution ($\sigma_\varepsilon = 0{\cdot}496$)

Spawning biomass B_T (1 000 t)	Minimum ε for positive apparent recruitment	Probability $\varepsilon < \varepsilon_{min}$
1	− 1·16	0·0096
500	− 1·11	0·0125
2 000	− 0·96	0·0262
4 000	− 0·79	0·0559
6 000	− 0·65	0·0951
10 000	− 0·41	0·2033

values of ε which give negative apparent recruitment for various levels of B_T. Some sample values, with their probabilities, are given in Table 6. While no instances of negative apparent recruitment have occurred in the time series of CalCOFI spawning-biomass estimates, there appears to be no reason, other than low probability, for such a condition not to be observed in the future.

Catch will be given as a function of spawning biomass, which could either reflect levels of nominal fishing effort, or in this case, be controlled by a variable quota management system of the form

$$Q = \begin{cases} a\,(B_T - b), & B_T - b > 0 \\ c, & \text{otherwise} \end{cases} \tag{26}$$

where Q is a reduction fishery quota, b is minimum spawning biomass for a quota to be established, and a is a fraction of the excess spawning biomass over level b. The quantity c is a small maintenance fishery for non-reduction uses such as live bait.

When we include exploitation of prespawners in the stochastic model, the equations become lengthy. The quantity R_{T+1} which is given by (25) is substituted into (9) to give an expression relating catch to B_T, ε and F:

$$Y = \frac{F}{F+M-G} B_T \left[1 - e^{-(F+M-G)}\right] + \omega \left\{ e^{\varepsilon} \left[\frac{1}{B\infty} + \left(\frac{1}{B_T} - \frac{1}{B\infty} \right) e^{-r} \right]^{-1} - B_T e^{-(M-G)} \right\} e^{(M-G)\tau} \frac{\varphi F}{\varphi F + M - G} \left[1 - e^{-(\varphi F + M - G)\tau}\right] \tag{27}$$

MARKOV MODEL

While the stochastic model could be investigated by Monte Carlo simulation methods, the model is uniquely adaptable to treatment as a Markov process, which can directly provide probability distributions of observed biomass. Various discrete levels of biomass can be treated as states. Since the model contains no time lags, transition probabilities between states are stationary.

For a vector of n discrete observed biomass values $B_1, \ldots, B_n$ (in ascending order), we wish to calculate the elements of a matrix containing the probabilities that a population of observed size B_i at time τ will become a population of observed size B_j at time $\tau + 1$. The probabilities of each possible transition are associated with the corresponding error term ε_{ij}, which has the properties described in the stochastic population model.

Since we are given that the observed biomass at time τ is B_i and the observed biomass at time $\tau + 1$ is B_j, Equation (8) provides us with

$$B_j = B_i\, e^{-(F+M-G)} + R_{T+1}\, e^{-\varphi F \tau} \tag{28}$$

where R_{T+1} is given by (25). Therefore,

$$B_j = B_i\, e^{-(F+M-G)} + \left\{ e^{\varepsilon ij} \left[\frac{1}{B\infty} + \left(\frac{1}{B_i} - \frac{1}{B\infty} \right) e^{-r} \right]^{-1} - B_i\, e^{-(M-G)} \right\} e^{-\varphi F \tau}$$

or

$$\varepsilon_{ij} = \ln \left(\frac{\left[B_j - B_i e^{-(F+M-G)}\right] e^{\varphi F \tau} + B_i e^{-(M-G)}}{\left[\frac{1}{B\infty} + \left(\frac{1}{B_i} - \frac{1}{B\infty} \right) e^{-r} \right]^{-1}} \right). \tag{29}$$

In implementing the Markov model on a computer, (29) can be substituted for ε in (27), so that F can be estimated iteratively given B_i, B_j, and Y_i. This value of F then gives ε_{ij} from (29), and a probability can be computed for the transition. Note that Y_i is determined by B_i and the quota formula (26). Each different quota formula will give a different and unique transition probability matrix.

The Markov model was based on a 30×30 probability matrix. Discrete biomasses were a geometric series from $B_1 = 200\,000$ t to $B_{30} = 16\,000\,000$ t, with an element ratio (s) of 1·16312. The probability associated with ε_{ij} was calculated from a fixed value of B_i, and an interval centered about B_j:

$$P\,(\varepsilon_{ij}) = \mathfrak{F}(B_j \sqrt{s}\, B_i) - \mathfrak{F}(B_j / \sqrt{s}\, B_i) \tag{30}$$

where $\mathfrak{F}$ is the cumulative density function for the normal distribution. The probabilities corresponding to the tails of the distribution were assigned to $\varepsilon_{i,1}$ and $\varepsilon_{i,30}$, respectively. The quantity $\mathfrak{F}$ was calculated by a polynomial approximation.

Each harvest policy (26) generates a unique transition probability matrix. Any probability vector associated with the vector of discrete observed population sizes B can be multiplied by the transition probability matrix to obtain a new vector of probabilities reflecting the likelihood of observing the corresponding population sizes in the following year. This multiplication can be used to investigate the probable near-term effects of management decisions. In the case of an infinite time horizon, which could be appropriate to long-term management policy, we can find the stable probability distribution to which all beginning probability distributions tend to converge after repeated multiplication by the transition probability matrix. This stable probability distribution is that eigenvector of the transition probability matrix whose eigenvalue is 1. Actually, after about 10 multiplications by the transition matrix, most initial probability vectors converge to very nearly the stable probability distribution given by the eigenvector.

While the model is at present used to evaluate alternative pre-specified quota policies, other uses are possible. If an objective function can be specified, the Markov model could serve as a basis for determining the optimum harvest policy (Mendelssohn[3], MS). In a management mode, the model can provide an *a priori* probability distribution so that biomass could be estimated by efficient Bayes methods.

Table 7. Comparison of resource characteristics under three harvest policies, and under the special case of an unequal sex composition in the landings. Values in million short tons

Harvest	Minimal (I)	Optimal (II)	Heavy (III)	Optimal (II) (sex ratio 1·73♀ : 1♂)
Slope (a)	–	0·33	0·33	0·33
Cutoff (b)	–	1·00	0·50	1·00
Maintenance (c)	0·01	0·01	0·01	0·01
Assumed maximum	0·01	1·00	1·00	1·00
Spawning biomass characteristics				
Median	3·35	2·05	1·66	1·84
Mean	4·12	2·75	2·35	2·48
Standard deviation	2·95	2·32	2·19	2·15
Probability (percentage of years)				
$B < 0{\cdot}5$	1·3	4·4	8·7	5·7
$B < 1{\cdot}0$	6·6	18·4	28·2	22·3
$B < 1{\cdot}5$	14·9	34·5	45·3	39·8
$B < 2{\cdot}0$	24·6	48·4	58·3	54·1
$B < 2{\cdot}5$	34·4	59·6	67·9	65·0
Yield characteristics				
Median	–	0·351	0·387	0·280
Mean	–	0·442	0·467	0·393
Standard deviation	–	0·379	0·362	0·370
Probability (percentage of years)				
$Y = 0{\cdot}01$	100	18·4	8·7	22·3
$Y < 0{\cdot}1$	100	28·2	15·9	33·1
$Y < 0{\cdot}5$	100	59·6	58·3	65·0
$Y < 1{\cdot}0$	100	80·0	80·3	83·7

Example Application

Three fishery management policies will be examined and compared (Fig. 8, Table 7). A "no fishery" policy (Case I) allows only 10 000 short tons' annual harvest for live bait and fresh-fish markets. This policy allows the biomass to remain at virgin levels and forms a basis for comparison. The "present" fishery (Case II) was recently adopted by the United States as an optimum yield policy, wherein the greatest overall benefit arises from maintaining a biomass somewhat larger than that resulting from a strictly maximum yield policy. A maximum yield or "heavy fishing" policy (Case III) passes through the peak of the equilibrium yield curve. Theoretically the largest yield would be obtained by a policy with a very steep slope and a fishery cutoff at about 1·5 million short tons. That policy would produce a highly variable fishery, whereas our Case III seeks to stabilize the fishery by virtue of a shallower slope and a lower fishery cutoff point.

When plotted on a log scale, the stable probability distributions resemble normal density functions (Fig. 9). The discontinuity at the tails of the distributions is slight. Under a minimal fishery (Case I), the highest probabilities are associated with biomasses near $B\infty$, as expected. However, the variability of the biomass is high, with a 25% probability of observing a biomass of less than 2 million short tons in any given year (Table 7). As fishing becomes more intense, the peak biomass shifts to lower values, and the probability distributions become flatter. Mean yield from Case III is only 6% greater than that from Case II; however, the mean biomass is 14% smaller, showing little marginal value from the heavy policy, especially if benefits arise from increased biomass. The lower fishery cutoff point of Case III results in fewer years of fishery closures, but at the same time would delay recoveries from periods of low abundance. Expected values and variances of more complicated fishery measures, such as economic yield, are easily calculated if the measure can be expressed in terms of biomass and catch.

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[3] Roy Mendelssohn, NMFS, Honolulu, Hawaii, USA.

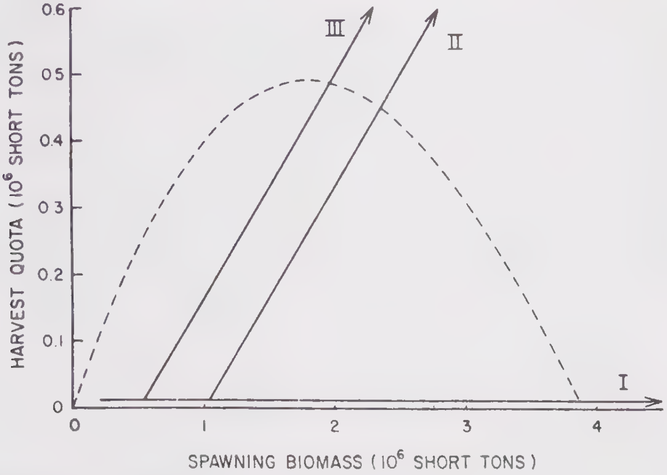

Figure 8. Three harvest policies examined by the model: I, minimal fishing; II, optimal fishing; III, heavy fishing.

DISCUSSION OF THE STOCHASTIC MODEL

Previous estimates of potential yield from the northern anchovy central stock have been based on the Gulland (1970) approximation formula. A wide range of potential yields was given, depending on the base years for determining "virgin biomass" (MacCall, Stauffer, and Troadec, 1976). Reasonable estimates ranged from 1 to 2 million short tons per year. The model developed in this paper suggests a much smaller potential yield of about 450000 short tons per year. In view of the historical low biomasses of anchovy, the Gulland potential yield estimates seem high, and are clearly not sustainable. The present estimate of potential yield seems somewhat low when compared with fisheries on similar species. However, many of those fisheries have subsequently experienced severe depletion, and the expectations may have been too high.

This model emphasizes the role of natural population variability in fishery projections. While the equilibrium yield curve from the deterministic model indicates a maximum yield of 484000 short tons, the stochastic model shows that somewhat less than this can be expected, and only under a highly fluctuating fishery. Yields of 200000 to 300000 t are more nearly sustainable in the strict sense.

In any particular year, abundance is determined by natural variations in recruitment, and a fishery will have little effect. However, over the long term, a fishery strongly modifies the probability distribution of biomasses. When a period of low abundance occurs under a fishery, one must not simply blame it on the fishery nor explain it away as an unavoidable natural event. In actuality, low abundance must be interpreted as a natural event which has become more likely because of the fishery. Management policies which do not reduce fishing pressure at low population sizes greatly increase the probabilities of low population sizes, often to the point of virtual certainty. The California sardine fishery, which had no effective constraint on fishing pressure or harvest, is such a case. An inflexible constant quota, even if set at a level below maximum equilibrium yield, contains a large risk of prolonged or possibly irreversible low population sizes.

The management policy adopted for the northern anchovy central stock (Fig. 8, Table 7) attempts to maintain an average population somewhat larger than that producing strictly maximum yield, by means of a harvest quota formula (26). Biomass was seen as contributing benefits by providing forage to other consumable and non-consumable predators, by providing more readily available supplies of live bait for recreational fishing, and by reducing harvesting costs of the reduction fishery. A reserve spawning biomass of 1 million short tons serves to preserve the reproductive capacity of the resource during adverse periods, and should help maintain some stability of trophic relationships in the ecosystem. When the resource is abundant, the allowable harvest will increase.

This variable quota policy is very resistant to errors in the model predictions. If the resource is more productive than anticipated, a larger biomass will obtain, and allowable harvest will increase. Similarly, if the resource is less productive, there will be a smaller average biomass and a smaller harvest. Random

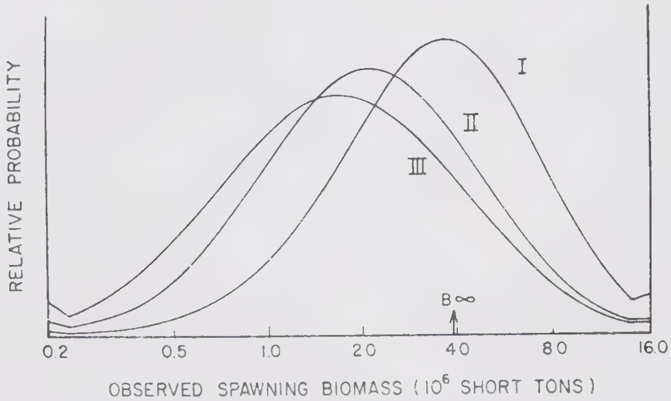

Figure 9. Spawning biomass probability distribution for three harvest policies.

variability is likely to produce periods of apparent high productivity and periods of apparent low productivity. Biomasses are serially correlated, protracting these periods somewhat longer than might be expected from random runs alone. A very large number of years will have to pass before the model can be adequately tested against actual resource performance.

There is considerable imprecision in the variability predicted by the model. The small number of observations results in a wide confidence interval. The substitution of observed biomass for actual biomass in the calculations results in an overestimate of resource variance, the actual biomass being less variable than our imprecise estimates. However, positive serial correlation in recruitment strengths is likely, although none was detected in the short time series which was available. As an extreme case of serial correlation, we must consider possible changes in the oceanic "regimes", as may have occurred in the late 1940s and early 1950s. Such serial correlation will increase the variability of population size, and the model predicts a lowering of average population size and yield.

A further error in the model predictions arises from the assumption that the fishery impact on the spawning biomass is measured by total yield. The fishery for the northern anchovy is peculiar in that the sex ratio of landings has averaged 1·73 females to each male by weight, whereas the population itself appears to be evenly distributed between the sexes (Klingbeil, 1978). Thus it appears likely that the fishery may have a disproportionate impact on the biomass of female fish, and therefore on the spawning potential of the population. If this hypothesis is true, the expected yield and biomass will be less than anticipated (Table 7), and the resource may be overfished with respect to the stated goal of optimum yield. As a corollary, management which encourages the harvesting of male fish could potentially increase yield at little loss to population size, and a more optimal utilization of the resource would result.

SUMMARY

The low anchovy central stock biomass in the early 1950s was probably due to a series of reproductive failures rather than to competition from the Pacific sardine. The pattern of anchovy population growth since 1951 can be empirically described by a logistic growth curve, which forms the basis of a population growth model. Estimated maximum equilibrium yield (484 000 short tons/year) is higher than maximum growth rate (353 000 short tons/year) due to competing risk of death and discontinuous reproduction. Asymptotic maximum spawning biomass is 3·9 million tons. A stochastic population growth model was derived from the deterministic logistic model by considering error in annual population size predictions. This model was implemented as a Markov process with various biomasses as states, and stationary transition probabilities based on a given harvest policy. The stable probability distribution indicates that the resource is highly variable in a natural unharvested state. Management policies can be examined by the model, providing expected values, variances, and probabilities of various events or conditions. The present management policy of allowing a reduction fishery to harvest one third of the excess over 1 million short tons' spawning biomass could be expected to have a mean annual yield of 443 000 short tons and a mean spawning biomass of 2·75 million short tons. Because the fishery harvests a disproportionate amount of females, there may be a corresponding disproportio-

nate impact on spawning potential, in which case the above management policy may result in overfishing with respect to the desired goal of optimum yield.

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THE CONSEQUENCES OF CANNIBALISM IN THE STOCK-RECRUITMENT RELATIONSHIP OF PLANKTIVOROUS PELAGIC FISHES SUCH AS *ENGRAULIS*

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INTRODUCTION

Recruitment in clupeoid fishes is usually highly variable (see Sharp, this volume, also Cushing, 1971; Cushing and Harris, 1973). This variability obscures the nature of the underlying relationship between the expected value (in the statistical sense) of recruitment and the abundance of the parental stock. A wide variety of mathematical models of the relationship have been proposed, but in very few cases have empirical observations been sufficient to justify a choice between models. While greater awareness of "The Stock Recruitment Problem" has been gained in the last two decades, remarkably little progress has been made in solving it. As a case in point, the classic debate between Frances N. Clark and John C. Marr (Clark and Marr, 1955) regarding density dependence versus independence in the stock-recruit-relationship of the Pacific sardine (*Sardinops sagax caerulea*) is being renewed in discussions regarding management of the northern anchovy (*Engraulis mordax*) fishery which succeeded it in California.

No doubt, given a long time series of data, empirical stock-recruitment models can be developed. However, in management's quest for maximizing consumptive benefit from most of these fisheries, we are faced with two problems: 1) an incorrect interim choice of management strategy is likely to terminate collection of the necessary data due to collapse of the fishery; and 2) overly conservative management is usually unacceptable due to pressing social and economic needs which can be met by fishery expansion. In this context, we cannot simply choose to wait until sufficient data have been accumulated to justify a particular empirical model; given the natural variability of recruitment, this approach could require more than a century. The alternative is to attempt to elucidate the mechanisms determining recruitment, and to construct rational "cause-and-effect" models.

This paper examines one cause-and-effect mechanism which leads to a characteristic family of stock-recruitment curves. While it is often difficult to demonstrate specific density dependent mechanisms by which clupeoid populations are regulated (albeit weakly), cannibalism is indisputably such a mechanism. The following discussion of cannibalism includes a variety of species, but the clearest and most complete information is available for the genus *Engraulis*.

THE RICKER CURVE

Ricker (1954) developed what has come to be known as the "Ricker curve" to describe a stock-recruitment relationship wherein initial production of offspring is proportional to stock size, but their subsequent mortality rate is also proportional to adult stock size. One common form of the Ricker curve is:

$$R = aSe^{-bS} \tag{1}$$

where R is recruitment, and S is spawner abundance. Fitted coefficients a and b reflect density independent and dependent factors respectively. In particular, coefficient b describes the proportionality between spawner abundance and the instantaneous coefficient of mortality of offspring up to the age of recruitment. Two mechanisms by which mortality is likely to be proportional to parental abundance are 1) cannibalism by the parents themselves (ibid), and 2) food limitation, whereby the length of time spent in some vulnerable stage is proportional to the initial number in this stage, and the mortality rate is constant over this time (Chapman, 1973). *Engraulis* eggs and yolk sac larvae would only be subject to cannibalism, but feeding larvae are conceivably subject to both density dependent mechanisms.

The food limitation mechanism is difficult to study. Probably the first step would be to demonstrate the existence of sufficiently small coherent patches of larval fish food such that predation by the larvae is a significant determinant of the density of food in the patch. Current thinking (Lasker, 1978) is that favourable food patches are very large with respect to distances travelled by larvae, i.e. larval ambits. An alternative possibility which is presently being investigated (J. Trent, Scripps Institution of Oceanography, personal communication) is that larvae are able to successfully feed on the cloud of plankton that surrounds particles of "marine snow". The size of these food patches is sufficiently small that feeding by larval fish could affect local food density. This mechanism will not be discussed further here.

Cannibalism has been the rationale for using the Ricker curve in models of several engraulid and clupeid populations, but its appropriateness has not been justified quantitatively; cannibalism has not been shown to be of sufficient magnitude to account for an appropriate portion of the mortality of spawning products. More often the Ricker curve is used because it appears to fit the data. Schaaf and Huntsman (1972) fit a Ricker curve to Atlantic menhaden (*Brevoortia tyrannus*) data with no discussion of an underlying mechanism. Murphy (1966, 1967) fitted Ricker curves to Pacific sardine data, citing cases of cannibalism by that and other species of *Sardinops*.

Gulland (1973) suggested that the Ricker model may be appropriate for the Peruvian anchoveta (*Engraulis ringens*), again based on non-quantitative considerations of cannibalism. Gulland suggested that mortality from cannibalism could, in principle, be determined from detailed examination of stomach contents. At the Third Session of the Panel of Experts (Instituto del Mar del Peru, 1973), J. Csirke presented a Ricker curve fit to catch per unit effort (CPUE) indices of adult and recruit abundances, but the mechanisms were discussed in only general terms. Interestingly, nearly all of the data points fell on the descending limb of the stock-recruitment curve. This tendency for recruitment to decline at increasing stock sizes clearly dictated rejection of a monotonically increasing stock recruitment curve such as that developed by Beverton and Holt (for a comparison of Ricker and Beverton-Holt curves, see Ricker 1973, 1975).

Csirke (1980) modified the usual Ricker curve in order to better distinguish between density dependent and independent mechanisms assumed to underly the model. Density independent processes were assumed to be a function of anchoveta stock abundance as calculated by cohort analysis (VPA). He realized that density dependent processes indeed were a function of density (biomass per unit volume or area) rather than overall abundance. Csirke's method of quantifying this difference was ingenious; he utilized CPUE as an index of density, effectively taking advantage of the very problem which has made CPUE a poor index of abundance of pelagic fishes. Csirke's model will be discussed further in a later section. As before, Csirke assumed that cannibalism is the most likely mechanism determining the shape of the stock-recruitment relationship. He cited several reports of stomach contents, some of which indicated extensive consumption of spawning products.

QUANTIFICATION OF CANNIBALISM

Until recently quantification of the impact of cannibalism has been difficult because little was known about egg production. Hunter and Goldberg (1980) have resolved this problem by histological analysis of anchovy gonads. The frequency of occurrence of one-day-old post-ovulatory follicles led them to conclude that *E. mordax* spawned every 6 to 8 days during the peak of the season. This allows daily production to be compared with estimated consumption of spawning products over a similar period. Hunter and Kimbrell (In press) have attempted such calculations. Based on a mean of 5.1 eggs per stomach and an instantaneous coefficient of gastric evacuation of 0.701/hr., they estimated daily consumption to be 85.8 eggs, or 5.1 eggs/g of fish weight. This compares with an average batch fecundity of 29.7 eggs/g for all fish (including males).

If we think of cannibalism as analogous to fishing, the catch equation describes the relationship between consumption ("catch"), initial abundance and rates of mortality. Thus we have

$$C_c = E_o F_c (1 - e^{-(F_c + M)t_e})/(F_c + M) \qquad (2)$$

where C_c is daily egg consumption per gram of adults (5.1 eggs/g)

E_o is daily egg production per gram of adults (29.7 eggs/g)

F_c is coefficient of mortality due to cannibalism

M is coefficient of mortality due to other causes, and

t_e is length of time eggs are subject to mortality, i.e. time to hatching

Two estimates of instantaneous coefficient of total mortality (Z) for anchovy eggs are available. Hunter and Kimbrell used an estimate given by Smith and Lasker (1978) of about 53%/day (Z = 0.775). This is an average over the years 1951 through 1969 and includes a wide range of anchovy abundances. The second estimate of Z is based on extensive sampling of egg abundance-at-age (Stauffer and Picquelle, 1980). This estimate of Z = 0.39 is somewhat lower and is associated with a level of anchovy abundance similar to that presumed to exist in 1976 and 1977 when Hunter and Kimbrell obtained their samples. Under typical conditions (ca. 15°C), anchovy eggs hatch in about 2.5 days (Theilacker, this volume). For purposes of the present calculations, I assume that a single day's consumption of eggs from the past three days' cohorts is equivalent to the consumption over three days of a single cohort. For the larger estimate of Z (Smith and Lasker, 1978), F_c is 0.153, and accounts for 20% of total mortality. The smaller estimate of Z gives an F_c of 0.108, accounting for 28% of total mortality.

These estimates of F_c allow evaluation of the significance of cannibalism to the stock-recruitment relationship of anchovy. The Ricker curve (Equation 1) has a maximum when $S = 1/b$ (Ricker, 1973). At this stock size the density dependent term is e^{-1}, and the survival rate from density dependent sources of mortality is 36.8%. If cannibalism is the only source of density dependent mortality, recruitment is maximal when

$$\int^{t_R} F_c(t)\, dt = 1 \qquad (3)$$

That is, when the age specific coefficients of density dependent mortality ($F_c(t)$) integrated over the time from spawning to recruitment (t_R) is equal to unity. If the integral exceeds unity, recruitment will decrease because of density dependent effects. This provides a convenient reference level for assessment of density dependent effects. If we evaluate the above integral over the egg stage alone (2.5 days), we obtain values of 0.383 and 0.270 for our two estimates respectively. Thus, in the egg stage alone, this accounts for one-third of the "reference" level of density dependent mortality.

Similar calculations are difficult to make for larvae. Hunter and Kimbrell (in press) report that anchovies digest small larvae beyond recognition in 30 min., so the apparent residence time is very short. Also, with digestion proceeding this rapidly, many larvae could be decomposed between the time the adult is captured and when the preservative effectively stops digestion. For example, midwater trawls for adult *E. mordax* are often 20 mins., in duration, and retrieval of the net takes another 20 mins. By the time the samples are preserved, at least 30 mins. have elapsed since the average time of capture. This indicates that only the larger larvae could resist digestion long enough to be observed, which is consistent with reported stomach contents. If cannibalism on larvae is to be quantified, rapid sampling methods will have to be developed. One possibility is a preservation system acting in the cod end of the sampling net.

In the absence of quantitative data on larval mortality caused by cannibalism, I offer the following speculation. The instantaneous coefficient of total mortality of *E. mordax* larvae has been estimated by Smith and Lasker (1978) as 0.14, and by Hewitt (In press) as 0.16. This is considerably lower than estimated egg mortality rates (also see Jones and Hall, 1974); it seems reasonable that rates of cannibalism will decrease similarly. Anchovy eggs and larvae are patchily distributed at all ages; however, patchiness is minimal at an age of about 18 days (Hewitt, In press). Dispersion may help decrease the rate of cannibalism, as the schools of adult anchovies orient preferentially to concentrations of food. However, anchovy larvae are susceptible to cannibalism for many weeks. The one measurable anchovy larva encountered by Hunter and Kimbrell (In press) was 17 mm, which corresponds to a likely age of over 30 days based on the growth curve given by Hunter (1976). If the average daily coefficient of mortality due to cannibalism were as low as 0.02, its action over 30 days would account for enough additional density dependent mortality to reach or exceed the "reference" level of 1.

The only comparable observations (i.e. quantified and taken during the spawning season) for the Peruvian anchoveta are reported by Rojas and Ochoa (1973). Rojas and Ochoa did not encounter anchovy larvae in the anchoveta stomachs, but did encounter 235 anchoveta eggs in 95 stomachs taken at four stations (I have omitted their station 52 in which the stomachs were nearly empty). The average stomach therefore contained 2.5 anchoveta eggs, or about one-half that observed by Hunter and Kimbrell. Rojas and Ochoa hypothesized a minimum feeding rate of three times per day, which is considerably less than Hunter and Kimbrell's gut evacuation rate would suggest. However, Rojas and Ochoa also indicated that phytoplankton may be digested more rapidly than zooplankton, and feeding rates could be generally higher for phytoplankton. Because *Engraulis* eggs are of a size that is usually consumed by filter-feeding (O'Connell, 1972; Hunter and Kimbrell, in press), we may expect higher rates of cannibalism when adults are filter-feeding upon phytoplankton. Because no egg production rate estimates are available for the Peruvian anchoveta, no firm conclusions can be drawn from Rojas and Ochoa (1973).

MODELS OF CANNIBALISM

Effective rates of cannibalism are undoubtedly influenced by a wide variety of factors, such as adult size, distribution and behaviour, adult and larval food quality and concentration, and abiotic factors such as mixing and temperature. It would be premature to attempt to treat all of the possible factors in a cannibalism model, given our present limited knowledge. Rather we may gain an indication of the nature, direction, and perhaps magnitude of these influences based on very simple models. These simple models may also provide some insight as to appropriate management of cannibalistic planktivores.

Hunter and Kimbrell (In press) argued that a random filtering model could not describe the apparent consumption rate of eggs. Under simple assumptions of habitat volume and egg density, they found that an anchovy would have to randomly filter from 17 to 25 h/day, which they interpreted as indicating non-random, selective feeding behaviour. This does not mean that we should not begin a modelling effort with a random filtering model. Contrary to Hunter and Kimbrell, a random filtering model may be sufficient to approximate the effects of cannibalism as a regulatory mechanism. It would certainly form a reasonable point of departure for construction of cannibalism models based on non-random filtering behaviour.

The following models assume the time of year to be the spawning season. Many stochastic considerations will be omitted so as to limit the scope of the discussion to the fundamental framework. Initially, the models will consider only local dynamics. A more integrative view is presented in the discussion following development of the models.

Random filtering model for eggs

A cohort of eggs will be subject to mortality from cannibalism, with rate coefficient F_c, and to the rest of natural mortality, including predation and starvation, with rate coefficient M, as in Equation (2). The rate of cannibalism is given by

$$F_c = Nvp/V \qquad (4)$$

where N is number of adult fish (cannibals)
v is average volume of water filtered per fish per unit time
p is fraction of time spent filtering, including fraction of habitat occupied by eggs,
and V is habitat volume

The egg mortality rate is therefore given by

$$dE/dt = -E(M + F_c)$$

or

$$dE/dt = -E(M + Nvp/V) \qquad (5)$$

Upon integration we obtain the number of eggs (E_h) surviving the period in the egg stage (t_e), i.e. the number of eggs that hatch.

$$E_h = E_o e^{-(M + Nvp/V)t_e} \qquad (6)$$

The initial abundance of eggs (E_0) is the product of the number of fish and the average individual fecundity (f), including males and prespawners. This gives

$$E_h = fNe^{-(M + Nvp/V)t_e} \qquad (7)$$

This equation has the form of a Ricker curve (Equation 1)

where
$$a = fe^{-Mt_e}$$

$$b = vpt_e/V$$

and number of eggs hatching is analogous to recruitment.

In modelling the events influencing the abundance and survival of pelagic fish larvae, initial conditions must include the number of eggs effectively hatched into the larval environment, which will be called "effective fecundity". Effective fecundity (E_h) can be divided into pre-spawning and post-spawning components. "Virtual fecundity" is the number of eggs released into the environment, and as Tsukayama and Alvarez (this volume) have shown, this component can be a compensatory function of population size, i.e. $E_0 = f(N)N$. The second component involves the subsequent survival of spawning products. Natural mortality and cannibalism will reduce the number of eggs which actually hatch to produce larvae. Again, cannibalism clearly leads to compensatory changes in effective fecundity as a function of population size or density.

As stated previously, the Ricker curve has a maximum when the density dependent exponent is equal to unity. Thus effective fecundity will be maximal when

$$Nvpt_e/V = 1$$

or
$$Nvpt_e = V \qquad (8)$$

That is, effective fecundity is maximal when the local population filters a volume of water equivalent to the habitat volume exactly once during the length of time it takes the eggs to hatch. Note that the location of the maximum is independent of natural mortality, although the value of the maximum is not.

Note that intensity of cannibalism is associated with fish density (N/V) rather than abundance alone. The density of fish which maximizes effective fecundity according to this model can be compared with actual fish densities. This provides an independent test of whether cannibalism is likely to be an important factor in population regulation. Johannesson and Vilchez (this volume) give most of the information necessary to perform the calculations. They base their biomass estimates on anchoveta averaging 6.7 g. Leong and O'Connell (1969) estimate that an *E. mordax* of this size would filter 1.64 l/min, and I will assume that this is valid for *E. ringens* as well. If time to hatching is 2.5 days, each fish would be capable of filtering 5900 l in this period. One metric ton would contain 150 000 fish, so one ton could filter 0.88×10^9 l in 2.5 days. Johannesson and Vilchez report that most of the biomass was detected in the upper 40 m of the water column. One square nautical mile at this depth would contain 1.37×10^{11} l. If filtering were random and continuous over the entire 2.5-day period (p = 1.0), maximum effective fecundity would correspond to a density of 156 tons/mile^2. Johannesson and Vilchez found average anchoveta densities of 600 or more tons/mile^2 in the years 1973, 1976 and 1978. Local densities reached much higher levels, occasionally exceeding 2000 tons/mile^2. Even if p is small, cannibalism is likely to have a significant effect on the proportion of anchoveta eggs being hatched.

Recruitment model

As was discussed previously, cannibalism continues for at least one month following hatching, although the rate may be lower. Whereas the anchovy feeds on eggs by filter feeding, larvae are of a size which is captured by biting (Leong and O'Connell, 1969; O'Connell, 1972; Hunter and Kimbrell, in press). The ratio of biting to filtering activity varied with the relative abundance of large and small food particles. O'Connell (1972) estimated that the ratio of particle sizes in southern California waters suggested that biting activity could exceed 50% of the total feeding activity. While individual fish did not tend to alternate feeding modes when faced with a mixture of particle sizes, fish at the front of the school showed more biting activity, while fish at the rear of the school showed more filtering activity. Although it may be attractive to model biting and filter feeding as mutually exclusive events (the time spent consuming larvae cannot be spent consuming eggs, and vice-versa), a more practical approach is to assume that a school consumes all eggs and larvae in its path. Either approach requires more knowledge of school sizes and behaviour than is presently available.

If a model incorporating cannibalism on larvae were to be constructed, it would be analogous to the egg model (Equation 7). Larval life may be divided up into three periods: t_e is the length of the egg period, t_1 is the length during which larvae are subject to cannibalism, and t_r is remaining time to recruitment. Each period has a natural mortality coefficient, M_e, M_1 and M_r respectively. The model would now give expected recruitment (R) as a function of population size and density:

$$R = fNe^{-(M_e t_e + M_1 t_1 + M_r t_r)} e^{-Np(vt_e + ct_1)/V} \qquad (9)$$

where c is rate of cannibalism on larvae. Recruitment will be maximized when

$$Np(vt_e + ct_1) = V \qquad (10)$$

This is analogous to Equation (8), and may be interpreted similarly. If the appropriate unit of cannibalistic activity is the school rather than the individual fish, then recruitment will be maximal when a volume of water equivalent to the habitat volume is swept once by the schools over the period from spawning to end of vulnerability ($t_e + t_1$), assuming p=1. If the speed and average cross-sectional area of schools were known, it would be possible to attempt calculations similar to those for eggs.

Evaluation of terms

The recruitment model (Equation 9) contains three terms bearing on recruitment strength: fecundity, density independent mortality, and density dependent mortality. These terms are clearer if we transform the equation by taking logarithms:

$$\log_e(R/N) = \log_e f - \Sigma M_i t_i - (vt_e + ct_1)pN/V \qquad (11)$$

Here the coefficient of density independent mortality has been generalized to $\Sigma M_i t_i$, where an arbitrary large number of stages replace the three simplified stages in Equation 9.

Relative roles of the three terms in determining recruitment can be evaluated by considering probable values in Equation (11). Hunter and Goldberg (1979) estimate the batch fecundity of female *E. mordax* to be 389 eggs/g. If half the fish are female and they average 17 g, the average batch fecundity is 3 300 egg/fish per spawning batch. If females spawn once every 6-8 days during the spawning season (ibid), perhaps 15 batches are spawned, giving a total fecundity of 50 000 egg/fish for the year. Thus $\log_e$ is approximately 11. The previous discussion of density dependent mortality indicates that we should expect this coefficient to be approximately 1. For a short-lived fish such as *Engraulis*, the adult natural mortality rate commonly exceeds 50% annually. At 50%, the replacement level of recruitment is equal to the spawning stock, so $\log_e (R/N) \approx 0$. The only remaining value is $\Sigma M_i t_i$ for which there is no direct measure; however, it must be approximately 10 for Equation (11) to balance.

These values indicate that the ratio of density independent to density dependent factors (neglecting density dependent effects on fecundity) is 10 to 1. The preponderance of density independent influences tends to mask the relatively weak regulation of stock abundance. This is consistent with the large variability characteristic of clupeid and engraulid stocks. The large contribution of density independent variability does not allow the population to equilibrate at a stable level. Rather, equilibrium takes the form of a probability distribution of abundances centred about a mean value (see MacCall 1980, Sharp this volume). A production or equilibrium yield curve may be derived, but it should be used with caution: it must be interpreted in a probabilistic rather than deterministic sense.

Equation (11) also provides a framework for consideration of variability in recruitment. For a given population size, fecundity and density dependent mortality have fixed average values, with variability being dependent on environmental conditions. The probability distribution associated with the density independent term will tend to characterize recruitment at all population sizes. A variation in any $M_i t_i$ will have an equivalent effect on recruitment independently of the stage (i) in which it occurs. The final convolution of the probability distributions of $M_i t_i$ for all i may be complicated. For example covariance is possible, as in the case where the high density of esculent particles required for successful first feeding will tend to increase the probability of subsequent successful feeding and survival.

Alternatively, it may be possible to define a number of stages for which the probability distributions of $M_i t_i$ are independent. The sum of several such random variates ($\Sigma M_i t_i$) may approach a normal probability distribution according to the Central Limit Theorem. If variability in density independent mortality dominates overall variability, we would expect $\log_e (R/N)$ to approach a normal distribution. Recruitment itself would tend to be distributed log-normally about its expected value for a given stock size. There is little direct evidence to demonstrate the true probability distribution of recruitment; indeed, the proper regression function is seldom clear. Use of log-log transformation often yields a constant variance of recruitment over a wide range of stock sizes, giving some support to the hypothesis of log-normality.

DISCUSSION

These models employ parameterizations which simplify complicated conditions and processes. The following discussions are centred on various types of considerations and their associated parameters.

Effects of fish size

Whereas fish size has not explicitly appeared in these models, several parameters can conveniently be expressed as power functions of fish weight or length. Leong and O'Connell (1969) estimated that the volume of water filtered by *E. mordax* per unit time increases approximately as the square root of fish weight. Hunter and Macewicz (1980) have estimated that batch fecundity increases as the 1.6 power of ovary-free female weight of *E. mordax*. Collins (1969) fitted allometric weight-length curves for *E. mordax*, obtaining exponents very near 3.0 for anchovies from southern California, but exponents were smaller (2.7 to 2.8) for fish from central California. If we standardize these variables to length of southern California anchovies, weight increases as the 3.0 power, filtration volume increases as the 1.5 power, and fecundity increases as the 4.8 power.

These relationships allow the model to be expressed in terms of biomass rather than numbers of fish. Biomass (B) is given by number of fish multiplied by their average weight (w), so $N=Bw^{-1}$. For example, the above filtration volume relationship can be substituted in Equation (8) to give maximum effective fecundity as a function of fish weight and biomass:

$$B/V = \sqrt{w}/apt_e \qquad (12)$$

where a is a constant of proportionality in the filtration volume relationship. This indicates that optimum density of biomass is proportional to the square root of the average fish weight, or the 1.5 power of average fish length. In other words, if anchovies are physically large, a larger equilibrium biomass would be expected than if they are physically small. As corollary, insofar as a fishery reduces the average age, and therefore the average size, the optimum density of the resource itself may be diminished. This argument holds only for the filter feeding mode of cannibalism (eggs). Leong and O'Connell (1969) estimated that particulate feeding rate increased as the 1.1 power of anchovy weight. This relationship is more appropriate to cannibalism of larvae, and the analog of equation (12) would indicate that the relationship is nearly independent of fish size.

Habitat volume and fish density

The preceding models have been restricted to local effects. The overall stock-recruitment relationship is an integrative average over extensive geographic and temporal variability. Neither the population (density dependent effects) nor environmental conditions (density independent effects) are uniformly distributed. While effective fecundity and production of larvae is likely to conform to a Ricker curve for a local area, the overall stock-recruitment relationship will be different. Ricker (1975, p. 294) states that nonuniformity of spawner distribution is likely to result in a flatter dome and more gently inclined descending limb than the simple Ricker curve would indicate. Johannesson and Vilchez (this volume) clearly show the extent of this nonuniformity: "estimates derived from the 7302 cruise data showed that 55% of stock biomass was concentrated in only 13% of the total area of distribution. Likewise, during the cruise 7603, 36% of the biomass fell within only 3.4% of the total area." It may be worthwhile to undertake a simulation study to examine possible shapes of stock-recruitment curves arising from observed patterns of stock distribution.

Habitat volume is essentially composed of three dimensions: alongshore, inshore-offshore, and vertical depth. The first two can be combined as a geographic area inhabited by the stock. Engraulid and clupeid fishes often show a characteristic pattern of changes in distribution with changes in population size. Murphy (1977) states "all or nearly all of the (clupeoid) stocks contract their feeding and spawning range as the population is reduced". Specific examples of this pattern are given by Smith (1972) for *E. mordax*, and Santander (this volume) for *E. ringens*.

The relationship of this pattern to reproduction may be elucidated by the following model. Consider a set of n discrete parcels of water V_i, i = 1...n. The first parcel corresponds to the centre of population distribution, and subsequent parcels are at progressive distances from the centre. I assume that density independent mortality is least (i.e. conditions are most favourable for larvae) at the centre, and that conditions are progressively less favourable at greater distances from the centre. Within each parcel the stock-recruitment relationship is a Ricker curve (Equation 1), and each parcel has a density independent survival rate a_i which decreases in value as i increases ($a_i > a_{i+1}$). The total population ($N_{tot} = \Sigma N_i$) is distributed among the parcels, and each parcel has a coefficient of fish concentration $c_i = N_i/N_{tot}$. Coefficients of concentration are estimated from the distribution of population among the parcels.

Given the above model, I wish to estimate the vector of coefficients of concentration which will maximize recruitment for the entire stock, and to examine how this vector changes with population size. Without actually solving the equations, I will offer a heuristic argument that this model generates distribution patterns similar to those observed for clupeoids. At very low population sizes, most of the population will be in the first parcel, where reproduction will be the most successful. As the population size increases, density dependent mortality will reduce the per capita recruitment rate in the first parcel until combined mortality rates in the first parcel are equal to the density independent mortality rate in the second parcel. At this point the population will begin expanding into the second parcel. Each successive parcel will be similarly occupied. At each level of N_{tot} the vector of c_i will be such that the sum of density dependent and density independent mortality rates (i.e. the total mortality rate) will be the same for all parcels. Under this condition there is no reproductive advantage in migrating to another parcel. There should be some level of N_{tot} which maximizes total recruitment. Above this population size maximum recuitment would be obtained by shunting the excess spawners to the least favourable area (increasing c_n) but this will not happen as long as fish individually attempt to maximize their own reproduction.

As a result of this pattern of distribution, average fish density increases relatively more slowly than total population size. This suggests that clupeoid stock-recruitment relationships may be better described by a generalized Ricker curve such as

$$R = aNe^{-bN^c} \qquad (13)$$

where $0 < c \leq 1$. When c = 1, a Ricker curve results. As c becomes smaller, the ascending limb becomes steeper, and the peak becomes broader with a progressively shallower descending limb. Csirke's (1980) stock-recruitment model is nearly equivalent to equation (13). Catch per unit effort (C/f) for pelagic fishes may commonly behave as a power function of stock abundance,

$$C/f = \alpha N^{\beta} \qquad (14)$$

where $\beta < 1$ (MacCall, 1976; Ulltang, 1976; Gulland, 1977). Thus Csirke assumes that β is a useful approximation of c in equation (13). It should also be noted that MSY will be overestimated if stock-recruitment data are fit by a Ricker curve (c = 1) when the actual relationship is characterized by c < 1. This is because the latter curve has a less pronounced peak.

I have hypothesized that habitat volume changes with population size in order to maximize individual reproduction. The mechanisms by which habitat volume changes are not known. One likely possibility is a tendency for adults to follow gradients of increasing food concentration. Without specifying any actual processes, it is safe to say that population expansion and contraction may occur by partially different mechanisms. For example, random diffusion will increase the range of fish as age increases. There is considerable evidence that older anchovies are distributed more widely than young anchovies in southern California (Mais, 1974). Larval drift patterns may result in some areas receiving more recruits than others, resulting in a tendency to contract toward these areas. If there are different mechanisms for expansion and contraction, and if the balance of effects determines the stock distribution, then habitat volume for the same total population size is likely to be characteristically different for increasing and decreasing trends in abundance. Thus, we may expect to see a "hysteresis" in the trajectory of population sizes over a cycle of decrease and increase. The concept of a single underlying stock-recruitment curve may be inappropriate.

Another consequence of the above geographic model is that the apparent overall stock-recruitment curve varies with the pattern of fishery removals. Segments of the population residing in the central "most favourable" areas will be reproducing closer to the peak or on the descending limb of their local stock-recruitment curves, while peripheral segments will be reproducing on the ascending limb of their stock-recruitment relationships. This indicates that fishery removals from the periphery may reduce recruitment proportionally to the fishery harvest, while removals from the centre may have little effect or may even increase recruitment. The most productive pattern of fishing should be to fish central areas of high density, and to discourage fishing at the edges of the population. Dispersion and migration of the fish will tend to reduce the relative benefit of this geographic fishing strategy.

The preceding discussion has not addressed the aspect of depth as a determinant of habitat volume. Over much of the range of the Peruvian anchoveta, maximum habitable depth is determined by low oxygen concentration. Limiting concentrations of oxygen may be as shallow as 10 to 20 m in inshore areas off northern Peru (see Richman and Smith, in press). The depth and intensity of oxygen depletion is a function of the rate at which organic material falls out of the overlying water. By consuming large amounts of primary and secondary production in the surface waters, the anchoveta may reduce the rate of detrital fallout, thereby depressing the depth of limiting oxygen concentration. Thus, within a given geographic area, increasing density of anchoveta may result in increased habitat volume, and increased reproductive rate due to decreased intensity of cannibalism.

Effects of food and feeding behaviour

Intensity of cannibalism is closely linked to the feeding behaviour of adults. The following discussion examines this relationship from three standpoints: responses to food abundance and to food composition, and non-random feeding behaviour. These considerations affect the value of parameter p, the effective time spent feeding.

Clearly, the amount of time spent feeding will decrease as food abundance increases (O'Connell 1972). The relationship between these two variables is poorly known because of our lack of knowledge of digestion patterns. Hunter and Kimbrell (In press) assumed a constant rate of gut evacuation, but their data appear to support the existence of an initial period of reduced gut evacuation, perhaps lasting 1 hour. Such a delay would increase the average residence time from 1.4 hours to 2.4 hours, decreasing estimates of total consumption by 40%. Rather than a continuous feeding model, Rojas and Ochoa (1973) appear to support a batch-feeding model. Until gut evacuation patterns are better known, it is difficult to compare gut contents with concentration of food in the environment in order to estimate volume of water swept or length of time spent feeding.

Bakun and Parrish (this volume) have compared oceanographic characteristics of the Peru and California currents with respect to larval habitat. Their discussion indicates that Peruvian conditions are favourable to formation of microlayers of larval food (see Lasker, 1978) because the ratio of wind mixing to upwelling decreases toward the equator. To this I would add that the high densities of food may result in less water being swept during feeding, and a lower *per capita* rate of cannibalism (b in Equation 1), so the peak of the Ricker curve occurs at a higher density of anchoveta than for the northern anchovy off California. Also, because food density may vary on a local scale, it may be appropriate to modify the geographic model presented earlier so that coefficients of density dependence (b_i) also vary among water parcels.

El Niño conditions may pose a compounded problem for the anchoveta. Not only may the density of spawners be high due to crowding into areas of upwelling (i.e. N/V is high), but if food abundance is low, the fish will spend more than a usual proportion of their time feeding (p is high). This combination may result in greatly reduced recruitment due to intense cannibalism. It may be appropriate to harvest these El Niño-induced inshore concentrations of anchoveta in order to increase recruitment. However, if density independent mortality of larvae is high, it may be more appropriate to maximize adult survival to the following year.

Adult *E. mordax* will feed either by biting or filtering depending on the size of food particles and their relative abundance (O'Connell, 1972). Thus eggs will tend to be cannibalized in the presence of phytoplankton, which is filtered, and larvae will tend to be cannibalized when in the presence of adult zooplankton, which is bitten. Rojas and Ochoa (1973) suggest that digestive rates may be higher for phytoplankton than for zooplankton, in which case the fraction of time spent feeding (p) would be higher in the presence of phytoplankton.

For the purposes of the following discussion, random feeding implies that feeding activity is independent of the abundance of eggs or larvae in the water. Hunter and Kimbrell may have prematurely dismissed the utility of simple random filtering models. They argue that the assumption of random filtering necessitated an unrealistically large proportion of time be spent to give the rate of egg cannibalism that they observed. However, if the mean residence time of eggs in the anchovy gut is 2.4 hours rather than 1.4 hours (see above), estimated daily consumption, and accordingly estimated fraction of time spent filtering (17h) would decrease by 40% (10h). Hunter and Kimbrell's second argument was based on their estimate that 17% of daily egg production was consumed by cannibalism. If we substitute the values of F_c derived earlier in this paper (0.108 to 0.153), which are more appropriate to the calculation, the length of time spent filtering will drop by 10% to 36% from the 25 hours they estimated. These lengths of time spent filtering (10 to 22 h/day) are consistent with O'Connell's (1972) calculations of the length of time necessary to obtain a daily food ration by filtering in areas of food abundance off southern California.

Non-random feeding behaviour is more strongly indicated by Hunter and Kimbrell's comparison of mean number of eggs per stomach and egg density in the same area as determined by towed plankton nets. Consumption of eggs increases as the 1.6 power of egg abundance, although the true functional shape of the relationship is unclear. It seems reasonable to hypothesize that at low egg concentrations consumption by filter feeding is incidental, whereas at higher concentrations eggs may contribute to the stimuli which elicit filter feeding.

Non-random feeding is more likely as food patchiness increases. Lloyd's (1967) "mean crowding" is a measure of the density of individuals within a patch and is therefore closely related to the stimuli eliciting feeding by adult anchovies (Leong and O'Connell, 1969; O'Connell, 1972). Mean crowding decreases as overall population density decreases, while patchiness (Lloyd, 1967) is a measure of mean crowding relative to mean density. Hewitt (in press) has examined these aspects of the spatial pattern of *E. mordax* larvae, and has shown that Lloyd's patchiness decreases from 10 to 8 during the first three days following hatching. From spawning to a corresponding total age of six days, numerical abundance decreases by about 75% ($M_e = 0.4$, $M_l = 0.1$, $t_e = 2.5$). Assuming that the patchiness of eggs is the same as newly hatched larvae, the combined result is an approximately 80% decrease in mean crowding over the first six days of life. Thus, any potential tendency for concentrations of eggs or larvae to elicit a feeding response by adults should diminish rapidly with time. Correspondingly, random feeding models of cannibalism may provide sufficiently good approximations that non-randomness can be ignored or can be parameterized by an increase in the proportion of time spent feeding (p).

SUMMARY AND CONCLUSIONS

Major points discussed in this paper were:

1) The Ricker curve often has been used to describe clupeoid stock-recruitment relationships, but quantitative justification has been lacking.

2) Cannibalism is an important regulatory mechanism if $F_c t \geq 1$, where F_c is the coefficient of cannibalistic mortality and t is the length of time eggs and larvae are subject to cannibalism.

3) Quantitative information on stomach contents and spawning rates of *E. mordax* indicate that $F_c t$ is in the range of 0.27 to 0.38 for anchovy eggs. Further cannibalism on larvae may be of reduced intensity, but the total effect indicates that cannibalism is sufficiently intense to be a regulatory mechanism.

4) Cannibalism on eggs is represented by a random filtering model. The rate of cannibalism is proportional to adult abundance and is inversely proportional to habitat volume: stock density rather than stock size is the important consideration.

5) Acoustic surveys of Peruvian anchoveta have shown densities sufficiently high that cannibalism is likely to have had a significant effect on net egg production.

6) Rates of cannibalism on larvae are not known. A complete stock-recruitment model cannot yet be calibrated with respect to cannibalism.

7) Evaluation of terms in a complete stock-recruitment model for *E. mordax* indicates that total coefficients of density independent and density dependent mortality are approximately 10 and 1 respectively. The preponderance of density independent influences tends to mask the relatively weak regulation of stock abundance. Clupeoid stock-recruitment and production curves must be interpreted in a probabilistic rather than a deterministic sense.

8) If the intensity of density independent mortality is a random variable, and is independent for several different life stages, recruitment may tend to be distributed lognormally about its expected value.

9) Biomass density giving maximum net egg production is proportional to the square root of average adult fish weight.

10) The rate of cannibalism on larvae, for a given level of biomass, is nearly independent of average adult fish size.

11) Because clupeoids expand and contract their ranges with changes in abundance, adult fish density is not proportional to stock size. The standard Ricker model is not appropriate; a generalized Ricker model such as $R = aN\,EXP(-bN^c)$ is more realistic, where $0<c<1$. The standard Ricker model ($c=1$) will overestimate the maximum sustainable yield from clupeoid stocks.

12) Contraction and expansion of range with changes in total abundance is predicted by a geographic model wherein spawners cannibalize their young, density independent survival of young decreases toward the periphery of the range, and spawners distribute themselves so as to maximize individual reproduction. As adult density in the most favourable area increases, cannibalism causes the total larval mortality rate to increase until peripheral, poorer areas become equally attractive spawning locations.

13) The optimal distribution of spawners results is a constant total mortality rate of offspring throughout the inhabited range. This mortality rate is equal to the density independent mortality rate at the edge of the range.

14) This geographic model suggests that harvests taken from the center of the range will have a smaller impact on abundance than harvests taken from the periphery of the range.

15) If Peruvian anchoveta consume sufficient production to decrease the rate of detrital fallout, it may cause a deepening of the level of limiting oxygen concentration. A larger anchoveta stock may thereby increase its own habitat volume, and in turn increase its own reproductive potential.

16) Rates of cannibalism are likely to depend on the size and abundance of adult food organisms. The *per capita* rate of cannibalism may be lower for *E. ringens* than for *E. mordax* because the high density of food off Peru may result in less time being spent feeding.

Cannibalism is one of the important mechanisms tending to regulate the highly variable abundance of clupeoids such as *Engraulis*. An initial framework was constructed which allows integration of life history information, physiology, behaviour, and quantitative ecology into a theory of clupeoid population dynamics. Further work can proceed in many directions; perhaps the most important is to incorporate environmental variability in order to fully describe the volatility of clupeoid populations. Finally, a number of speculations and hypotheses have been presented. Some of these may be tested in the field or laboratory.

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SHORT COMMUNICATION

Geographic Location of Individual Pixels

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A major problem in processing thermal infrared digital data from very high resolution radiometers aboard NOAA Polar Orbiting Satellites is the geographic placement of digital data fields. Geographic placement is especially difficult over oceanic areas because of the lack of landmarks. Using a series of geometric constructions, an analytical approach can be developed for geographic location of individual data pixels. The errors associated with this method are generally less than 0.1° latitude and longitude.

Introduction

Kirkham and Stevenson (1976) presented a method for applying a given geographical grid-coordinate matrix (Bonner, 1969) to a computer-generated digital image. Accurate placement of the grid-coordinate matrix relative to the satellite data field is a critical part of this method. Previously, this required lining up a geographic grid overlay with a scanline/pixel overlay on the photographic image to identify an individual pixel. With NOAA-5 Very High Resolution Radiometer (VHRR) data, errors of up to 0.6° in latitude and longitude were found when using this procedure for the placement of the grid-coordinate matrix. This communication describes a method for analytically determining the geographic location of an individual data pixel to an accuracy of less than 0.1° in latitude and longitude.

Geometric Relationships

The geographic placement of the center pixel of a given scanline on the photographic image can be derived using an algorithm for the satellite orbit path subpoint location developed by Eber (1973). Since the spacecraft is in earth orbit and the satellite sensor scans perpendicular to the orbit path, the individual scanlines approximate great circle arcs over the earth's surface. The scanning rate of the instrument is sufficiently fast so that skewing of individual scanlines due to earth rotation is negligible and can be ignored (Legeckis and Pritchard, 1976).

The distance between the scanline subpoint and an individual pixel on that line is the great circle distance, *d*, and can be computed given the satellite sensor angle α (see Fig. 1). The angular range for the NOAA-5 VHRR is 66° from sync-line to sync-line and corresponds to 2912 pixels. The center pixel of each scanline is number 2666. Thus for a given pixel P the sensor angle α, in degrees, can be expressed by

$$\alpha = \frac{|P-2666| \times 66^\circ}{2912}. \tag{1}$$

The great circle distance in degrees of

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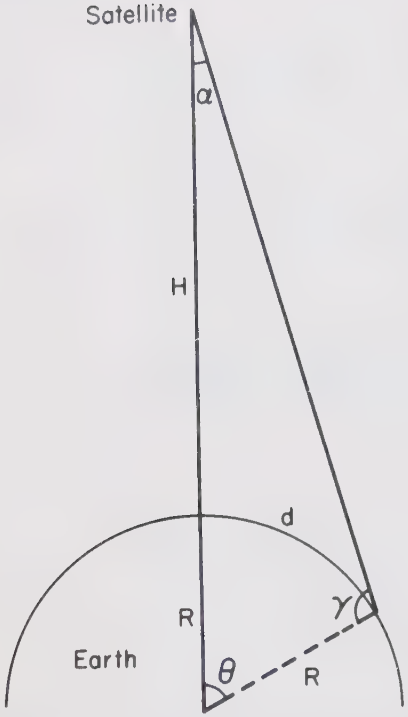

FIGURE 1. Relevant geometry for defining the great circle distance *d*.

latitude, d, can be computed as follows:

$$d = \frac{\pi R \theta}{180° \times 1.852 \times 60}, \qquad (2)$$

where

$\theta = \gamma - \alpha$,

$\sin \gamma = [(H + R)\sin \alpha]/R$,

H is the height of the satellite orbit (1511.4 km for NOAA-5),

R is the radius of the earth (an average of 6371.0 km),

α is the sensor angle as expressed in Eq. (1),

γ is the angle between the satellite and the earth's center at the individual pixel,

θ is the angle between the satellite and the individual pixel at the earth's center.

The scanline azimuth (Z_n) or angle relative to true north (see Fig. 2) is computed using the following equation (Legeckis and Pritchard, 1976):

$$\cos \varepsilon = \cos I / \cos L_1, \qquad (3)$$

where

I is the inclination angle at the equator,

L_1 is the latitude at the scanline subpoint.

If $P < 2666$ then $Z_n = \varepsilon + 180$. If $P > 2666$ then $Z_n = \varepsilon$.

Given the great circle distance, α, and the azimuth, Z_n (as shown in Fig. 3), we can solve the spherical triangle for the geographic latitude and longitude using the following formulas (Dunlap and Shufeldt, 1969):

$$\sin R = \sin Z_n \times \sin d, \qquad (4)$$

$$\cos |K - L_1| = \frac{\cos d}{\cos R}, \qquad (5)$$

$$\sin L_2 = \sin K \times \cos R, \qquad (6)$$

$$\sin t = \frac{\sin R}{R \cos L_2}, \qquad (7)$$

where R and K are intermediate points used for computational purposes only.

The result t is the difference in longitude between the scanline subpoint and the desired pixel. Thus the geographic coordinates of P are L_2 and $(\lambda_1 + t)$ if $Z_n > 180°$ or L_2 and $(\lambda_1 - t)$ if $Z_n < 180°$.

Results

Table 1 compares the location of individual pixels with known landmarks using both the analytical approach pre-

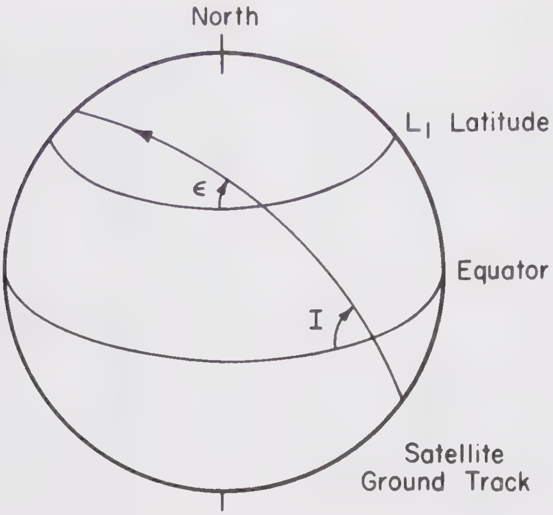
North
L_1 Latitude
ϵ
Equator
I
Satellite Ground Track

FIGURE 2. Geometry used to derive the scanline azimuth (Z_n).

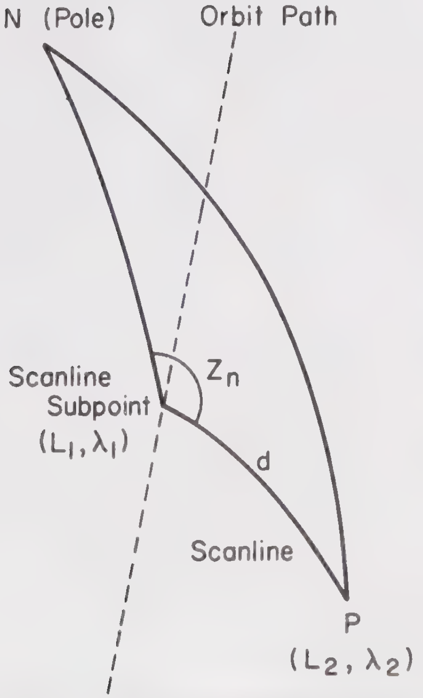
N (Pole)
Orbit Path
Scanline Subpoint
(L_1, λ_1)
Z_n
d
Scanline
P
(L_2, λ_2)

FIGURE 3. The spherical triangle used to compute the latitude and longitude at pixel *P*.

sented in this communication and the approach described by Kirkham and Stevenson (1976). A significant reduction in error of geographic placement is apparent using the analytical approach, which appears generally to be accurate to less than 0.1° latitude and longitude.

The grid-coordinate matrix generated by Bonner's program may be accurate over small areas such as a high resolution digital field, but for satellite photographic images where large distances are involved, location errors become significant. It is advisable to use an analytical approach to geographically identify a local area on a satellite photographic image before applying a grid-coordinate matrix to a digital field.

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TABLE 1 Comparisons for Pixel Location Using Both the Analytical Approach and The Grid Overlay Approach.

NOAA-5 ORBIT	SCAN LINE	PIXEL	CHARTED		COMPUTED		DIFFERENCES	
			LATITUDE	LONGITUDE	LATITUDE	LONGITUDE	LATITUDE	LONGITUDE
3268	4128	3232	34.03	120.35	34.05	120.37	−.02	−.02
3268	4198	3390	33.28	119.55	33.25	119.54	.03	.01
8120	4327	2347	36.63	121.93	36.56	121.83	.07	.10
8120	4677	3041	33.03	118.57	32.97	118.46	.06	.11
8145	4300	3341	36.63	121.93	36.56	121.97	.07	−.04

NOAA-5 ORBIT	SCAN LINE	PIXEL	CHARTED		GRID OVERLAY		DIFFERENCES	
			LATITUDE	LONGITUDE	LATITUDE	LONGITUDE	LATITUDE	LONGITUDE
3268	4128	3232	34.03	120.35	34.25	120.50	.22	.15
3268	4198	3390	33.28	119.55	33.45	119.75	.17	.20
8120	4327	2347	36.63	121.93	36.90	121.95	.27	.02
8120	4677	3041	33.03	118.57	33.45	118.20	.42	−.37
8145	4300	3341	36.63	121.93	37.25	121.35	−.62	.58

Naval Institute, Annapolis, Maryland, p. 62.

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REMOTE SENSING OF ENVIRONMENT 10:307–310 (1980)

Measuring Sea Surface Temperature from Satellites: A Ground Truth Approach

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Determining the correction for atmospheric attenuation is a major problem in processing thermal infrared digital data from very high resolution radiometers aboard NOAA Polar Orbiting Satellites. An empirical equation for estimating this correction is developed. The coefficients of the equation are determined by using regression techniques and comparing satellite observations to sea surface temperature measurements. Although there is not sufficient data to fully evaluate this procedure, initial satellite measurements are within 0.5°C of independent sea surface temperature measurements.

Introduction

Over cloud-free oceanic areas, the very high resolution radiometer (VHRR) aboard NOAA-5 and the advanced very high resolution radiometer (AVHRR) aboard TIROS-N, both observing the thermal infrared (10.5–12.5 μm), can provide imagery in which the thermal structure of the sea surface is quite evident. Digital data related to such imagery can be quantitatively processed and thus provide a means for monitoring the ocean environment from space. However, the temperatures derived after applying standard calibration procedures are still only equivalent black-body temperatures which are uncorrected for atmospheric attenuation. The first factor, pertaining to the nonblackness of the radiator, is not critical because in the 10.5–12.5 μm bandpass, the ocean radiates as a black body to a very good approximation. The second factor, correction for atmospheric attenuation, is quite critical and must be accounted for.

Classically, calculations to correct for the effect of atmospheric attenuation on the source signal as it propagates from the ocean surface to the satellite are made by measuring the volume of water vapor in the atmospheric column. The data for such measurements is obtained from radiosondes, which, unfortunately, are not frequently launched over oceanic regions. Other methods to correct for atmospheric attenuation include several semiempirical models (Breaker et al., 1978). But, after applying corrections derived by such models, the satellite measurements can still differ from the true surface temperatures by two or three degrees Celsius.

Correcting for Atmospheric Attenuation

A model to correct for atmospheric attenuation can be developed for use whenever sea-truth (ground-truth) temperatures are available. The derivation starts with a simplified form of the radiative transfer in the atmosphere,

$$B_0 = B_s \exp(-\tau) + B_i[1 - \exp(-\tau)], \quad (1)$$

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where

B_0 = brightness observed by the satellite,
B_s = brightness of the sea surface,
B_i = brightness of the atmosphere,
τ = optical depth of the medium.

Equation (1) defines the atmospheric attenuation over a given path directly below the spacecraft (a path through one atmosphere). For observations to the side of the satellite subtrack, the surface radiation is attenuated over a longer path. The distance of this path is a function of the instrument or nadir angle at the satellite, and the height of the atmosphere. This distance can be computed geometrically following Fig. 1 and is given by

$$a=\left[(h+R)^2-(H+R)^2\sin^2 n\right]^{1/2}-\left[R^2-(H+R)^2\sin^2 n\right]^{1/2} \qquad (2)$$

where

a = distance of attenuation path,
n = nadir angle,
H = height of satellite,
h = height of atmosphere,
R = radius of earth.

The height of atmosphere in this case can be assumed to be 100 km. The exact height is not critical, as what is needed is the distance ratio D given by

$$D=a/h \qquad (3)$$

Applying the distance ratio to the optical depth, Eq. (1) becomes

$$B_0=B_s\exp(-\tau D)+B_i[1-\exp(-\tau D)]. \qquad (4)$$

The atmospheric component (B_i) of eq. (4) is relatively small and is considered to be constant over a given area.

The Planck equation, which relates brightness to temperature, is nonlinear at thermal infrared frequencies. However, the error, as a result of linearizing the segment for local sea surface temperatures (10–20°C), is not significant. Thus replacing B by T, Eq. (4) becomes

$$T_0=T_s\exp(-\tau D)+C, \qquad (5)$$

where

T_0 = temperature observed by the satellite,
T_s = temperature of the sea surface,
C = constant temperature value.

Solving equation (5) for T_s yields

$$T_s=(T_0-C)\exp(\tau D). \qquad (6)$$

The coefficients required to correct for atmospheric attenuation (C and τ) can be computed by correlating the satellite measurements with sea truth using Eq. (6) as a regression equation.

Evaluating the Model

At the Southwest Fisheries Center, a computer program series is available for quantitatively processing satellite data. Each processing run covers a region that is approximately 140 km^2 on the earth's surface. The atmosphere is assumed to be homogeneous over the given region. Typically, only about 15 sea-truth measurements are available for regression analysis to determine the specific coefficients of the atmospheric correction equation. The statistics to this approach, as applied to a region off Monterey Bay

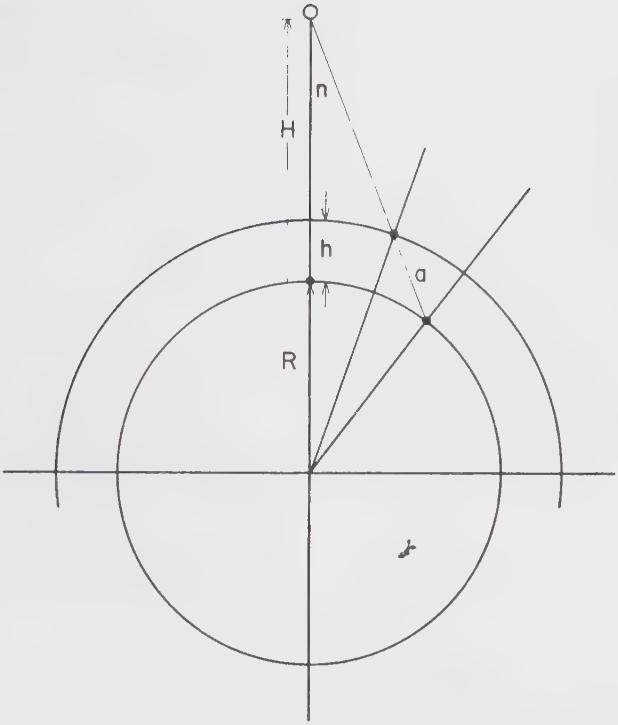

FIGURE 1. Atmospheric attenuation path.

taken from NOAA-5 orbit 8145, are listed in Table 1 where,

R = the coefficient of correlation between sea truth and satellite measurements,
$\bar{\Delta}$ = mean difference between sea truth and satellite measurements,
S_Δ = standard deviation of the difference,
N = number of surface measurements.

The statistics in the column labeled "uncorrected" describe the relationship between sea truth and satellite measurements which were not corrected for atmospheric attentuation. The statistics in the column labeled "Corrected" describe a similar relationship, but where the satellite measurements have been corrected for atmospheric attenuation using Eq. (6).

The statistics in Table 1 show the degree to which the data fits the equation used to correct for atmospheric attenuation. To fairly evaluate the use of such an equation, an independent source of data is needed. For the region involved, there were two independent sources of data available (see Table 2). During an unrelated survey conducted by NASA, two surface temperature measurements coinciding with the time of the satellite pass were taken. The measurements only differed from the corrected satellite values by 0.0 and 0.5°C, respectively. Another measurement, obtained from a drifter drogue deployed by the Scripps Institute of Oceanography, differed from the satellite measurement by only 0.4°C.

It is unfortunate that more data is not readily available to evaluate this approach. However, the results presented should indicate that suitable corrections

TABLE 1 Statistics Related to Satellite-Measured Sea Surface Temperature for NOAA-5 Orbit 8145

	UNCORRECTED	CORRECTED
R	0.84	0.93
$\bar{\Delta}$	0.06	0.01
S_Δ	0.80	0.46
N	14	14

TABLE 2 Independent Data Sources

CORRECTED SATELLITE	NASA	Δ
11.1	11.1	0.0
10.3	10.8	0.5

CORRECTED SATELLITE	SIO DROGUE	Δ
13.7	14.1	0.4

for atmospheric attenuation over a given region can be determined by applying regression techniques. The procedure offers a means for using satellite measurements to extrapolate beyond a ship's single point observation of sea surface temperature.

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Received 24 September 1979; revised 29 August 1980.

8055

MARINE ENVIRONMENTAL CONDITIONS
IN THE EASTERN NORTH PACIFIC OCEAN
January 1978 - March 1979

Douglas R. McLain[1] and W. James Ingraham, Jr.[2]

LARGE-SCALE MARINE CLIMATIC CONDITIONS

Atmospheric Circulation

Wagner (1979) described the atmospheric circulation and weather over North America during 1978. The winter 1977-78 and the first part of the winter 1978-79 continued a pattern of atmospheric circulation begun in 1976-77 in which a strong ridge of atmospheric pressure formed along the west coast with a trough downstream over the central or eastern United States (Fig. 1). This circulation continued the pattern of winter 1976-77, with mild temperatures and abundant precipitation in Alaska areas with cold, snowy weather to the east. During winter 1977-78 temperatures along the California coast were near or above normal and precipitation was abundant as the ridge allowed storms to move in from the southwest. During December 1978 and January 1979 the ridge formed again but was shifted to the west several hundred kilometers off the coast and extended northwards over Alaska. This allowed some northerly flow over the west coast, bringing below normal temperatures, especially over the southern part of California. By February 1979 the ridge shifted farther west and became an "omega type" blocking ridge over the Bering Strait (Dickson 1979). This led to the formation of a trough near the west coast which brought above normal precipitation to much of the coast.

Surface Pressure

Maps of the distribution of surface barometric pressure are available routinely from many agencies (see, for example, those published in Fishing Information); for brevity they are not reproduced here. These maps show the Aleutian low pressure system centered near the Aleutian Islands in winter with resultant westerly winds over much of the North Pacific. In spring and summer the low fills and weakens and the North Pacific high-pressure system expands from off California so that by August the high dominates the circulation of the northeastern Pacific. In fall the high-pressure cell contracts and the Aleutian low deepens and resumes its normal winter position over the Aleutians.

This annual pattern of pressure distribution occurred in 1978 and early 1979 with several variations. In early 1978 strong westerly winds occurred over much of the northeastern Pacific and apparently caused strengthened flow of the California Current. In September 1978 an isolated low-pressure system occurred in the Gulf of Alaska.

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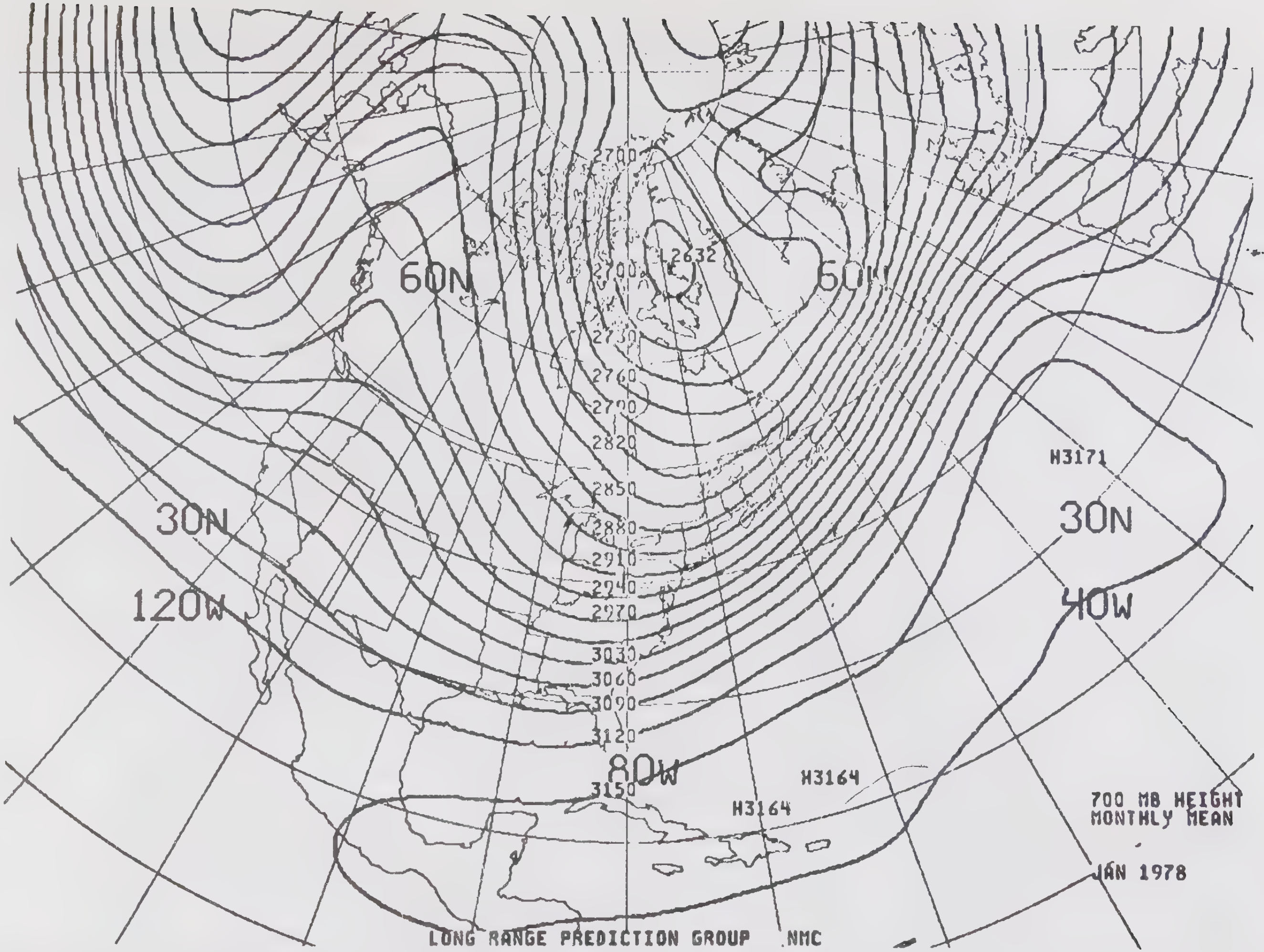
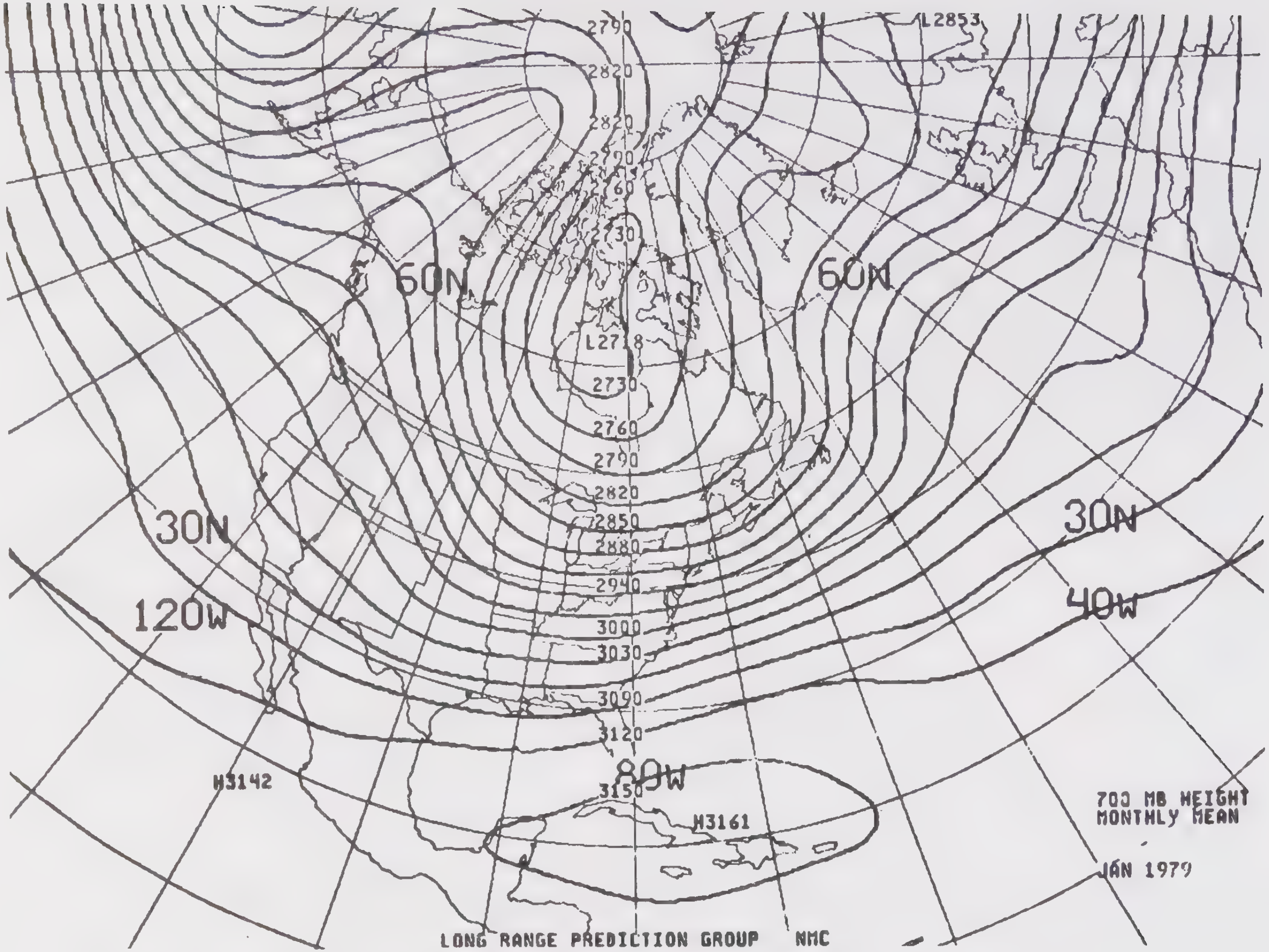

2700
2632
2700
2730
2760
2790
2820
2850
2880
2910
2940
2970
3030
3060
3090
3120
3150
60N
60W
30N
120W
30N
40W
80W
H3171
H3164
H3164
700 MB HEIGHT
MONTHLY MEAN
JAN 1978
LONG RANGE PREDICTION GROUP NMC

Figure 1.--Height of the 700 mb pressure surface (meters) in January 1978 (upper) and January 1979 (lower). From 30^{o}-60^{o}N the upper level winds flow generally west to east (midlatitude westerlies) parallel to the contour lines, carrying with them to some extent the air mass conditions of temperature and humidity of upstream areas. The closer the spacing of the contour lines, the steeper the height gradient of the pressure surface, and the


L2853
2790
2820
2820
2790
2760
2730
L2718
2730
2760
2790
2820
2850
2880
2940
3000
3030
3090
3120
3150
60N
60N
30N
30N
120W
40W
80W
H3142
H3161
700 MB HEIGHT
MONTHLY MEAN
JAN 1979
LONG RANGE PREDICTION GROUP NMC

faster the wind speeds; thus the farther downstream the upstream air mass characteristics may be carried. In general, under a pressure surface ridge or area of divergence of the contour lines, weather is fair, warm, and dry; under a trough or area of convergence of the contour lines, weather is likely to be cloudy, cold, wet, and stormy. Charts supplied by the Long Range Prediction Group, NWS, Washington, DC 20233.

In January 1979 an intense Aleutian low was present over the central Aleutians, while the North Pacific high was shifted to the west of its normal position, thus causing strong southwesterly winds in the region between it and the low. In February the low split into an eastern and western portion with the eastern portion centered over the Gulf of Alaska near southeastern Alaska.

Wind-Driven Transport

The oceanic surface layer transport due to surface wind stress is estimated monthly by calculations of wind-driven (Ekman) transport using monthly mean fields of surface barometric pressure. These data are summarized as vectors of transport by month at selected points in the northeast Pacific.[3] Figure 2 shows monthly vectors of computed transport for the 15 months January 1978-March 1979, while Figure 3 shows the long-term monthly mean vectors (January-March repeated).

During late 1977 and early 1978 there was stronger than normal northeastward Ekman transport in the Gulf of Alaska (57°N, 140°W) and northeastward rather than the normal southeastward flow at 50°N, 133°W. This northeastward transport moved water towards the shore, which resulted in downwelling along the coast of southeastern Alaska and British Columbia and caused a strengthening of the northerly flow along the coast. Biological implications included a massive intrusion of salps into the area. Strong northward transport occurred at 57°N, 170°W in the Bering Sea.

At the two locations, 39°N, 149°W and 27°N, 140°W, there was unusually strong southeastward transport in January-February 1978, and at 27°N, 140°W, the transport was also southeastward rather than the normal northward flow. These transports resulted from the strong atmospheric circulation over the eastern North Pacific during winter 1977-78.

Transports during spring and summer 1978 were near normal values with the exception of strong offshore transport off California (39°N, 128°W) during May-July.

During winter 1978-79 several large anomalous transports occurred. In the Gulf of Alaska (57°N, 140°W) transport was southeastward in early winter rather than in the usual northeastward direction. Very strong northward transport occurred at 57°N, 140°W in February 1979. South of Kodiak (50°N, 153°W) strong southeastward transport occurred in October and December. Off California (39°N, 128°W) there was strong southeastward transport in February 1979.

Upwelling

Bakun (1973) computed an index of coastal upwelling using the component of Ekman transport normal to the coastline at 15 locations along the west coast from the Gulf of Alaska to Baja California. Historical values of upwelling index are presented in Figure 4 for the period of record, 1946 to the present, as anomalies from the long-term mean of the reference period 1948-67. This period is used for various other data sets in this report and also is used as a reference period by Fishing Information. Positive values of the index represent upwelling, and negative values represent downwelling.

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[3] A. Bakun, Pacific Environmental Group, NMFS, Monterey, CA 93940. Values are computed on a grid of 3 degrees of latitude and longitude from data of Fleet Numerical Oceanobraphy Center, Monterey, CA 93940.

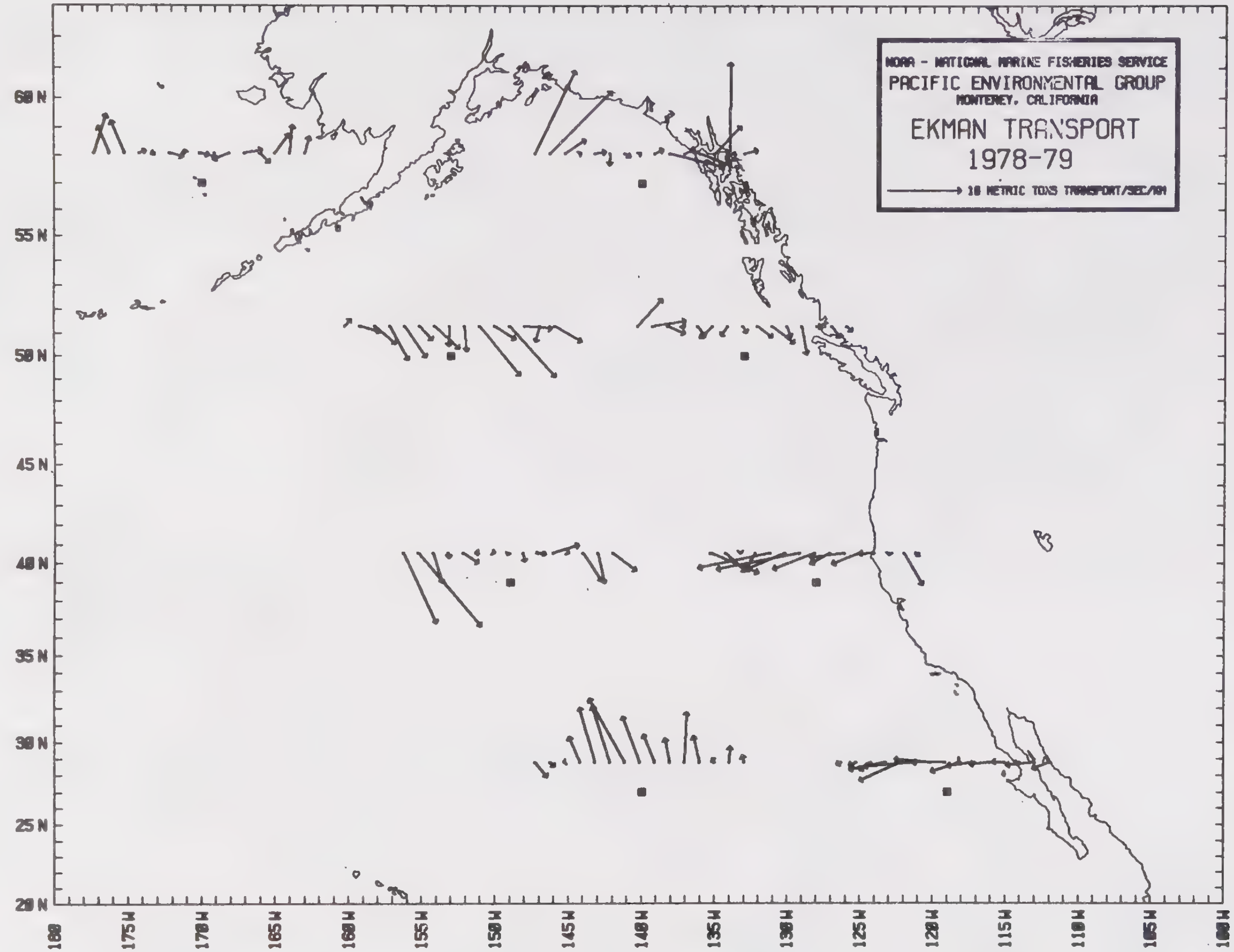

NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EKMAN TRANSPORT
1978-79
10 METRIC TONS TRANSPORT/SEC/KM
60 N
55 N
50 N
45 N
40 N
35 N
30 N
25 N
20 N
180
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W
125 W
120 W
115 W
110 W
105 W
100 W

Figure 2.--Vectors of monthly mean Ekman transport for 15 months during January 1978-March 1979 for selected points in the eastern North Pacific, computed over a 3-degree area of latitude and longitude. Points are shown as black squares. Data from A. Bakun, Pacific Environmental Group, NMFS, Monterey, CA 93940.

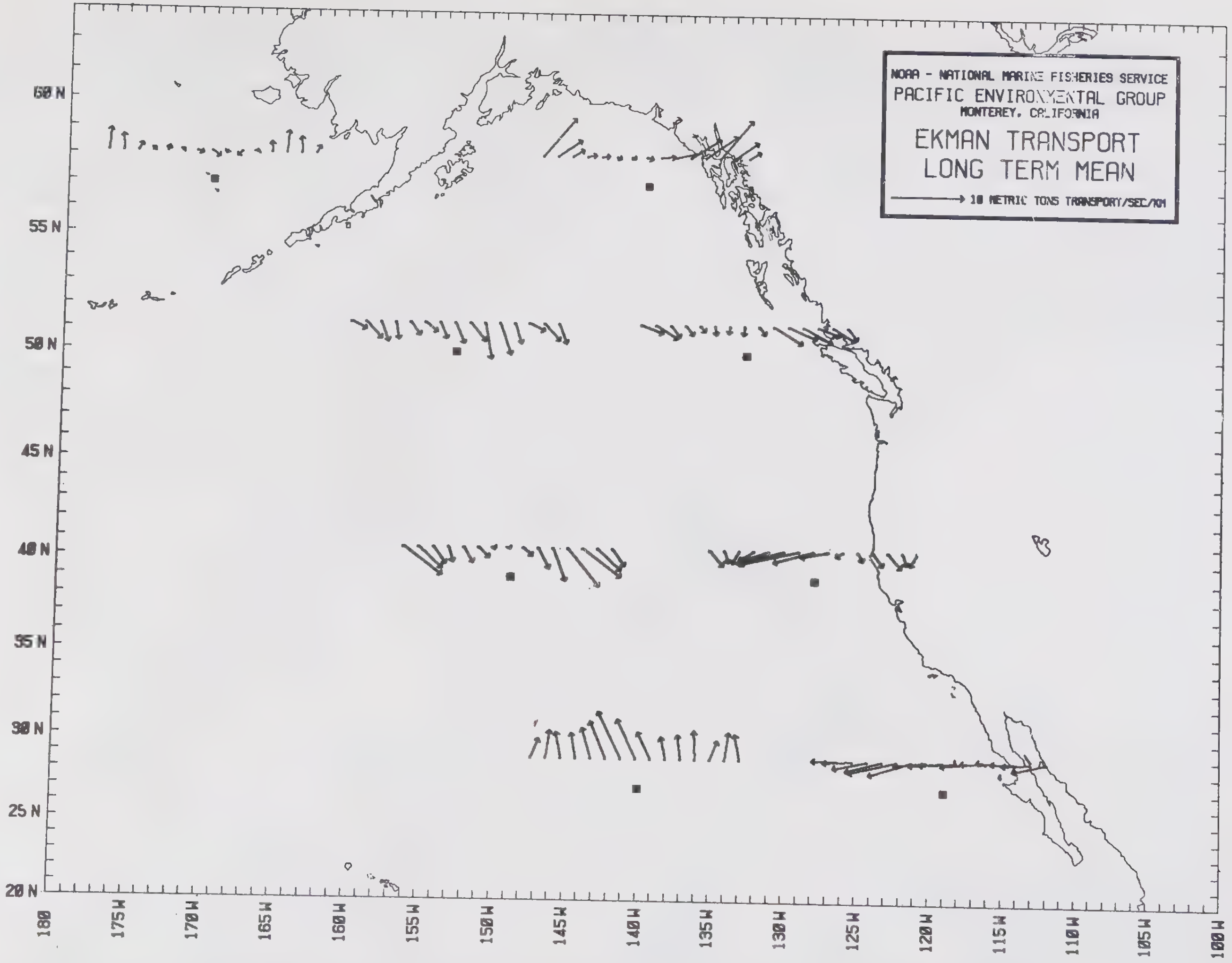

NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EKMAN TRANSPORT
LONG TERM MEAN
10 METRIC TONS TRANSPORT/SEC/KM
60 N
55 N
50 N
45 N
40 N
35 N
30 N
25 N
20 N
180
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W
125 W
120 W
115 W
110 W
105 W
100 W

Figure 3.--Long-term mean monthly Ekman transport for 15 months (January-March repeated) for the reference period 1948-67 for selected points in the eastern North Pacific, computed over a 3-degree area of latitude and longitude. Points are shown as black squares. Data from A. Bakun, Pacific Environmental Group, NMFS, Monterey, CA 93940.

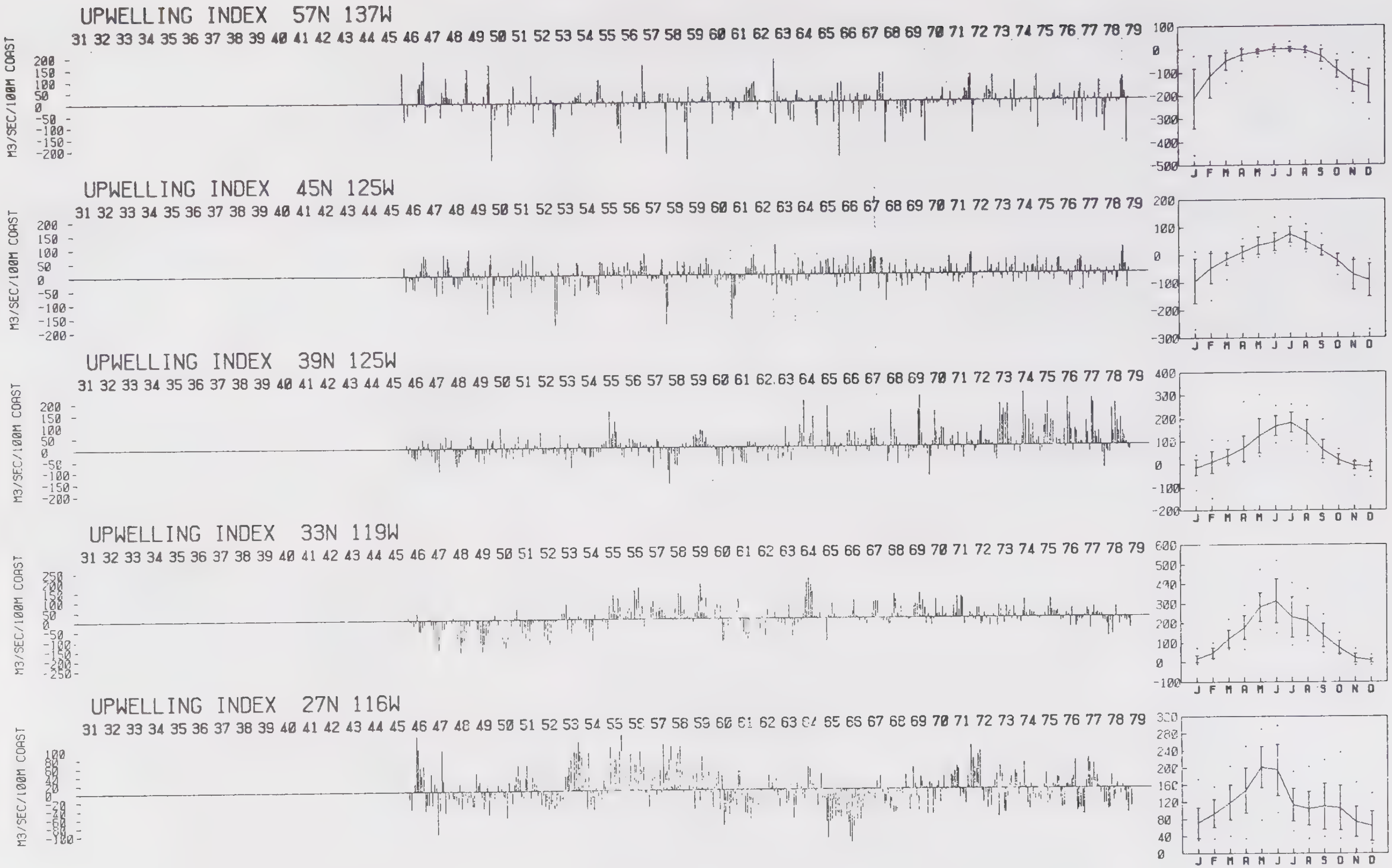


Figure 4.--Time series for 1931-79 of anomaly of upwelling index in cubic meters of water per second per 100 meters length of coastline from the long-term mean reference period 1948-67. Data from A. Bakun, Pacific Environmental Group, NMFS, Monterey, CA 93940. Small boxes on the right-hand side of this and other time series plots show the annual cycle with the range and standard deviation of interannual variations during the reference period.

The area of maximum upwelling along the west coast is centered near 39°N, 125°W (Bakun et al. 1974), although numeric values of the upwelling index are higher off southern California due to an effect of coastal mountains (Bakun 1973). For the sixth year in a row, upwelling at 39°N, 125°W was generally above normal during 1978. In early 1979 upwelling indices at 39°N, 125°W were near normal.

Farther south at 33°N, 119°W, upwelling indices have been near normal in recent years, whereas at 27°N, 116°W, values have been generally below normal. North of 39°N upwelling is less important and downwelling in winter becomes dominant. At 45°N, 125°W and 57°N, 137°W upwelling indices in recent years have been variable, but near normal values.

Details of the variations of upwelling indices in 1978 and early 1979 at all 15 locations along the coast are presented in Figure 5. The data are presented as percentiles of occurrence of values of upwelling index at that location over the period of record (1946 to date). By taking percentiles of the values, the data are normalized and can be intercompared. Low percentiles indicate increased downwelling or decreased upwelling while high percentiles indicate increased upwelling or decreased downwelling.

Although upwelling indices were generally high during 1978, at 39°N, 125°W during January-March they were below normal and were unusually low from 30° to 36°N. Extreme low index values occurred at 36°N, 122°W in January and from 30°N to 36°N in March. This was a case of predominant onshore transport and downwelling during a period of light or southerly winds associated with a persistent high-pressure system and drought conditions then occurring over California. The onshore transport apparently concentrated fish larvae near shore, as will be mentioned later.

During May-July upwelling conditions returned to more normal ranges. Upwelling was stronger than normal north of 51°N in June and north of 39°N in July. Weak upwelling occurred from 42°-54°N in August and September. Upwelling indices then returned to abnormally high values in October-December north of 36°N. Intense upwelling conditions in Gulf of Alaska waters may have resulted in anomalous offshore transports of fish larvae. During December 1978 and early 1979 onshore transport again occurred off central and southern California. This was a similar occurrence to that in early 1978, but was much less extreme.

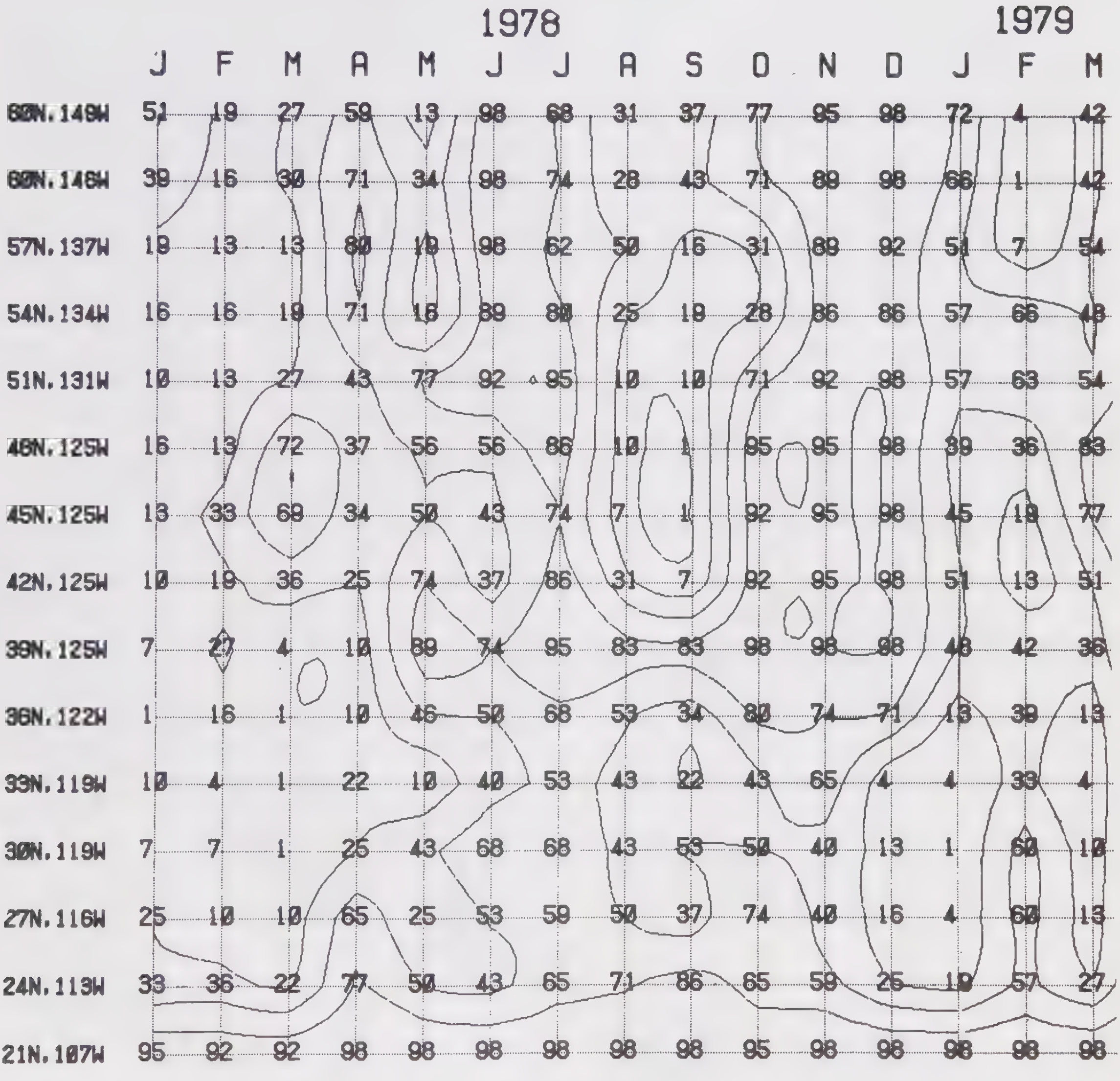
Extremely high upwelling indices were calculated at 21°N, 107°W throughout the period. Similar high values occurred during 1977. Because the high values occurred only at the one location, 21°N, 107°W, and not to the north, the data appear questionable; the cause is not known, but it may be due to a change in analysis procedures of the surface pressure observations.

Sea Level

Long historical records of tide height are available for many tide gage stations along the coast. Tide height is primarily affected by astronomical factors, but also by oceanographic and meteorological factors including variations in speed of alongshore currents (Reid and Mantyla 1976). Most of the tidal effects are relatively short-term and can be averaged out by making monthly means of the hourly tide height observations. Meteorological and long-term (nodal) tide effects can be compensated for, and thus tide height or sea-level data can be used to infer changes in ocean circulation.

Bretschneider and McLain (1979) presented monthly mean sea-level data for a series of stations along the west coast of North and South America from the Aleutian Islands to Chile. They showed that anomalies of monthly mean

PERCENTILIZED MONTHLY UPWELLING INDICES



	1978											1979		
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
60N.149W	51	19	27	59	13	98	68	31	37	77	95	98	72	4	42
60N.146W	39	16	30	71	34	98	74	28	43	71	89	98	66	1	42
57N.137W	19	13	13	80	10	98	62	50	16	31	89	92	51	7	54
54N.134W	16	16	19	71	16	89	80	25	19	28	86	86	57	66	48
51N.131W	10	13	27	43	77	92	95	10	10	71	92	98	57	63	54
48N.125W	16	13	72	37	56	56	86	10	1	95	95	98	39	36	83
45N.125W	13	33	69	34	50	43	74	7	1	92	95	98	45	19	77
42N.125W	10	19	36	25	74	37	86	31	7	92	95	98	51	13	51
39N.125W	7	27	4	10	89	74	95	83	83	98	98	98	48	42	36
36N.122W	1	16	1	10	46	50	68	53	34	80	74	71	13	39	13
33N.119W	10	4	1	22	10	40	53	43	22	43	65	4	4	33	4
30N.119W	7	7	1	25	43	68	68	43	53	50	40	13	1	60	10
27N.116W	25	10	10	65	25	53	59	50	37	74	40	16	4	60	13
24N.113W	33	36	22	77	50	43	65	71	86	65	59	25	19	57	27
21N.107W	95	92	92	98	98	98	98	98	98	95	98	98	98	98	98

Figure 5.--Monthly upwelling index values for January 1978-March 1979, in percentiles of the frequency distributions made up of the 34 values for each month and location in the 34-year (1946-79) time series. Locations in the Gulf of Alaska are toward the top of the figure; those off Baja California are toward the bottom. The contour interval is 25 percentiles. Values above the 50th percentile indicate stronger than normal upwelling, while those below the 50th percentile indicate weaker than normal upwelling.

sea level from a long-term mean are remarkedly coherent in time and space. In particular, they showed that periods of high sea level can be traced southward along the coast from Alaska to Chile and are associated with above normal sea-surface temperatures along the coast and with El Niño occurrences in the Eastern tropical Pacific.

Some sea-level data are available for west coast tide stations during 1978.[4] Anomalies of monthly means from the long-term mean are presented in Figure 6 for five stations with the most complete data records. Above normal sea levels occurred along the California coast in 1940-41, 1957-59, and 1972-73, as discussed by Bretschneider and McLain, and were associated with major El Niño occurrences. The periods of above normal sea level can be traced northwards to Alaska but are obscured there by effects of storms.

In 1976 there was a minor El Niño and high sea levels were observed at California stations in late 1976. High sea levels also occurred in the winters of 1977-78 and 1978-79, probably as a result of onshore wind-driven transport. Data from the northern stations, particularly Yakutat, AK, are incomplete, but show low sea levels in late 1978. Possibly higher than normal levels existed in early 1978 in response to onshore transport.

Sea-Surface Temperature

Spatial Variations - Analyzed maps of sea-surface temperatures (SST) and their anomalies from a long-term monthly mean are published monthly in Fishing Information and are not reproduced here. (also see Appendix.) These maps showed that a large pool of cooler than normal water formed in the northeastern Pacific during late 1977 and persisted into 1978. In early 1978 the pool was located at 35^{o}-40^{o}N, 140^{o}W to 180^{o}, and was bordered on the east and north by a coastal strip of warmer than normal water. By May the pool had expanded northward to the Alaska coast and by August it reached eastward to the California coast. Breakup of the anomaly pattern then began, and by December a warmer than normal pool occupied the central portion of the northeastern Pacific surrounded by cooler than normal water. This general pattern persisted through March 1979.

Temporal Variations - Johnson et al. (1976, 1978) presented time series plots of SST for selected 5-degree squares of latitude and longitude in the North Pacific. These squares, called Index Stations, were chosen because of a relatively large number of available ship weather observations. Johnson et al. chose 10 such areas along the coast of the northeast Pacific from the central Aleutian Islands to Equador (Table 1). Time series of SST for these areas for 1931-79 are shown in Figures 7 and 8 as anomalies from a long-term mean (1948-67).[5] Because of the scarcity of SST data from the Bering Sea, air temperature data[6] from St. Paul, Pribilof Islands, are also also included in Figure 7. Details of fluctuations of SST along the coast are discussed later.

SST's along the coast of North and

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[4] Provided by J. R. Hubbard, Tides and Water Levels Division, National Ocean Survey, NOAA, Rockville, MD 20852. Recent data are provisional and are based on preliminary datums. The time series of monthly mean sea levels have been detrended to eliminate long-term trends, and corrected for the inverse barometer effect of atmospheric pressure. The 19-year period 1949-67 was used as a long-term mean for sea level to correct for nodal tide effects (Bretschneider and McLain 1979).

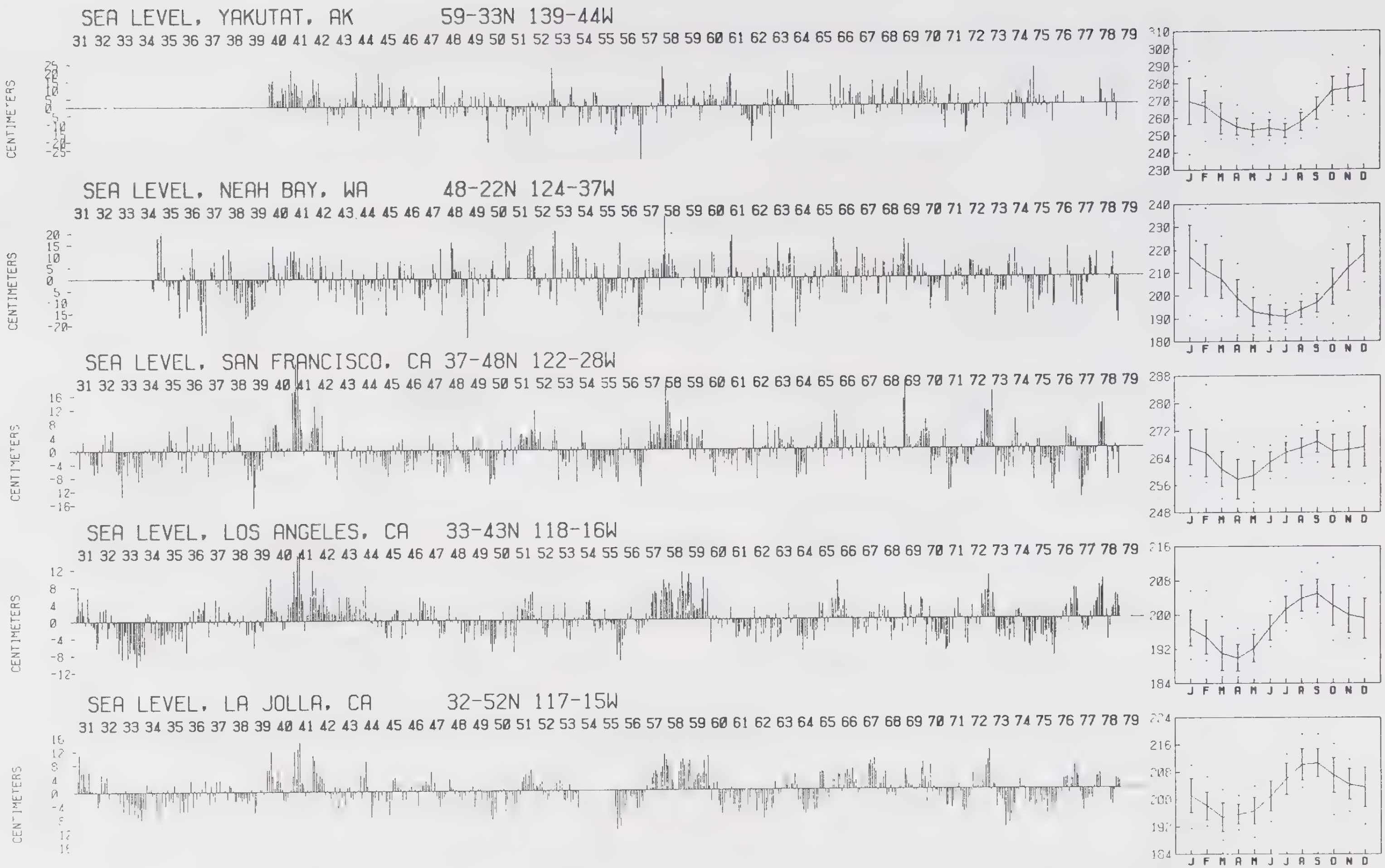

Figure 6.--Time series for 1931-79 of anomaly of sea level in centimeters from the long-term mean reference period 1949-67 at tide gages from Alaska to California. Data from J. R. Hubbard, National Ocean Survey, NOAA, Rockville, MD 20852.

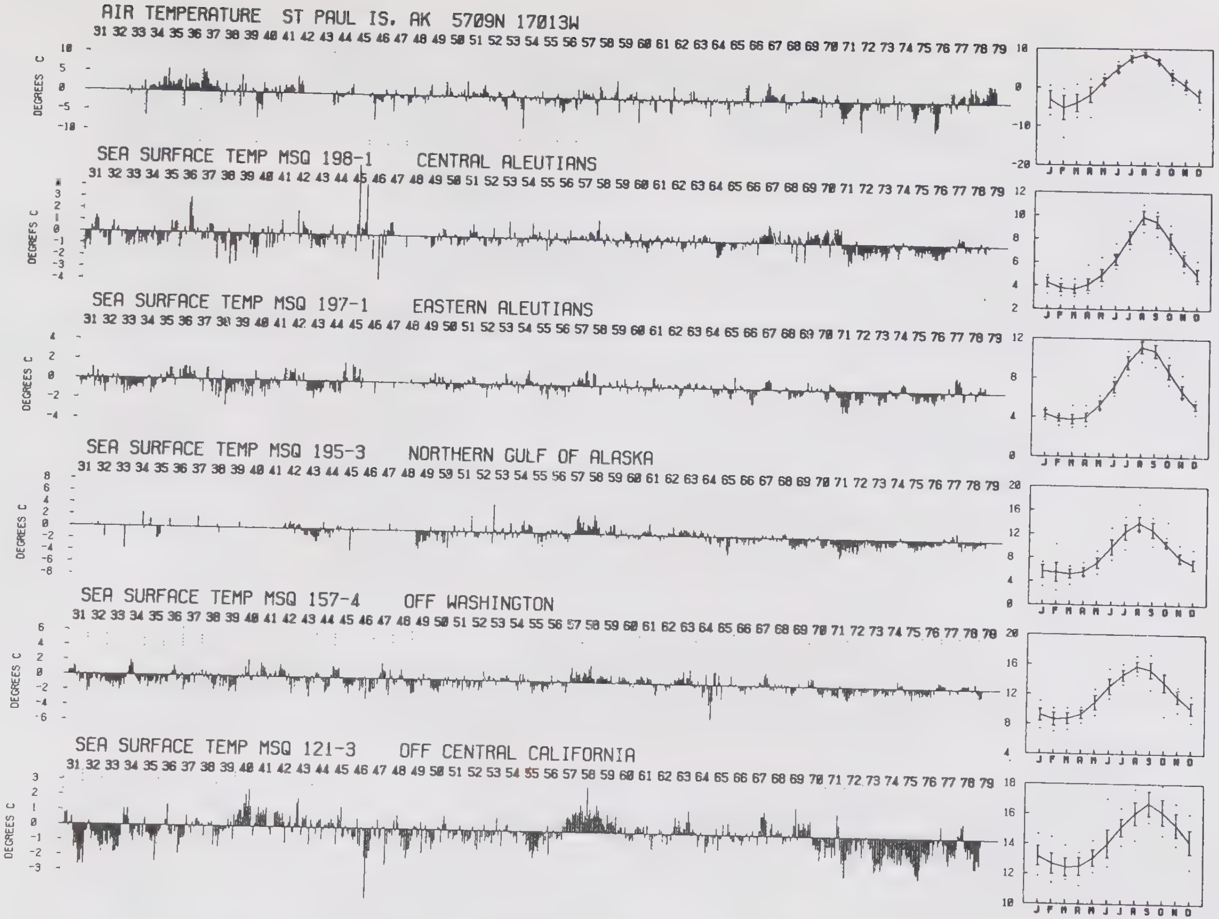

Figure 7.--Time series for 1931-79 of anomaly of air temperature in degrees Celsius at St. Paul Island, AK, and sea-surface temperature in degrees Celsius from the long-term mean reference period 1948-67 at five 5-degree squares of latitude and longitude along the coast from the Aleutian Islands to California. Air temperature data for St. Paul Island and sea-surface temperature data for 1931-71 from the National Climatic Center, EDIS, Asheville, NC 28801; SST data for 1972-79 from Fleet Numerical Oceanography Center, Monterey, CA 93940.

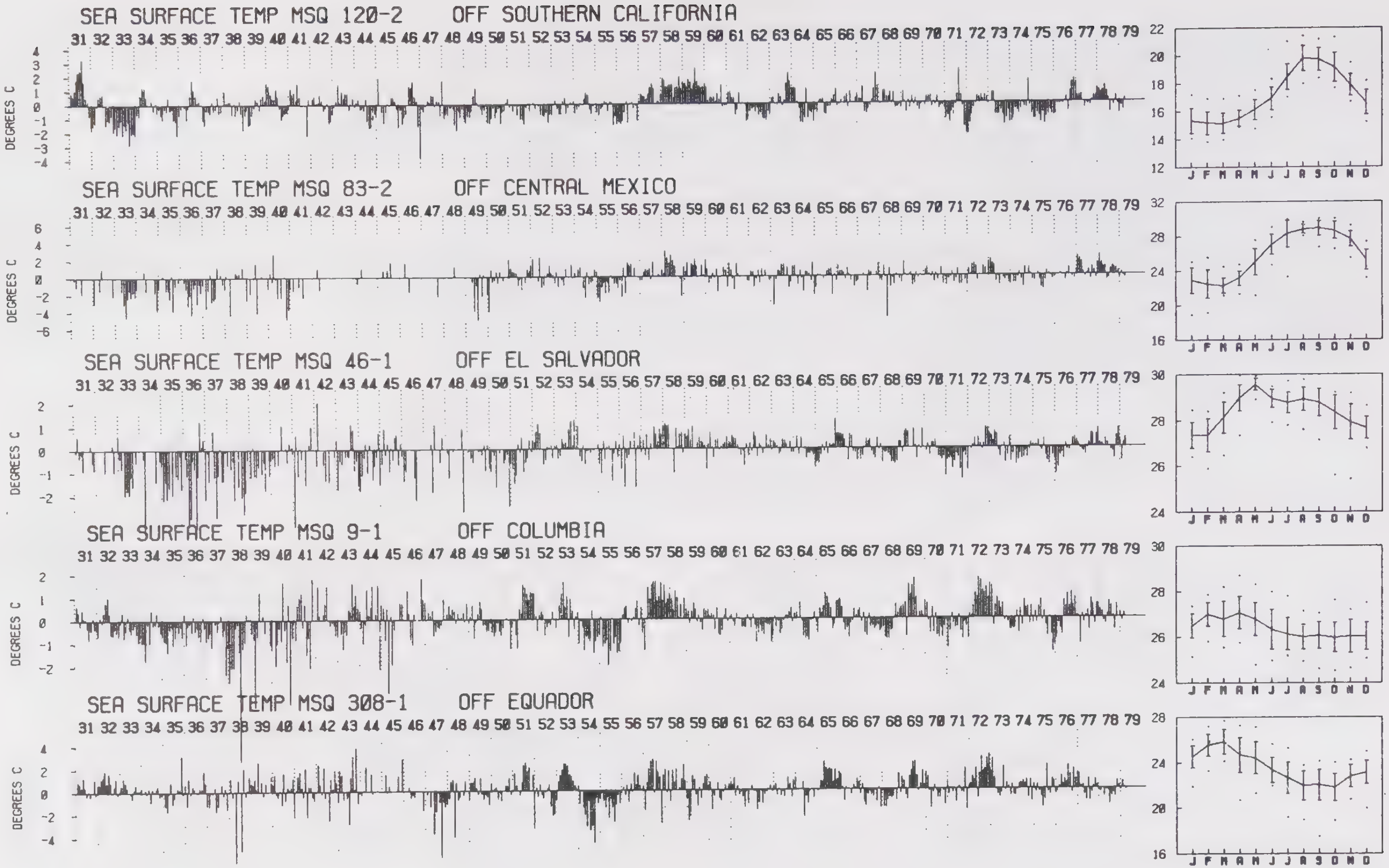

Figure 8.--Time series for 1931-79 of sea-surface temperature in degrees Celsius from the long-term mean reference period 1948-67 at five 5-degree squares of latitude and longitude along the coast from California to Ecuador. Data for 1931-71 from the National Climatic Center, EDIS, Asheville, NC 28801; data for 1972-79 from Fleet Numerical Oceanography Center, Monterey, CA 93940.

Central America have shown similar variations with time along extensive stretches of coast. Temperatures in the early 1940's and during 1958-59 were above normal over most of the coast, while temperatures in the early 1930's, late 1940's, 1955-56, 1970-71, and 1974-75 were below normal in most areas. The years 1972-73 and 1976 had above normal temperatures along the Central American coast in association with recent El Niño occurrences, but had near or below normal temperatures in the northern areas.

A prolonged period of below normal SST in the Bering Sea and Gulf of Alaska during 1971-76 was broken in 1977, and temperatures along the coast have been near or above normal since then. In early 1977 air temperature at St. Paul Island and SST from the Aleutians (square 198-1) to Washington (square 157-4) became near or warmer than normal. Off California, SST's remained generally below normal except for near normal temperatures off central California (121-3) and above normal off southern California (120-3) in the winter of 1976-77 and in early 1978. This pattern continued to the south off Central America with above normal temperatures in winter 1976-77 and early 1978. Off Ecuador (square 308-1), SST's have been near normal since 1977.

Table 1.--Locations of Index Stations for time series of sea-surface temperature data along the coast of the northeast Pacific Ocean.

Location	Latitude	Longitude	Marsden 5° square
Central Aleutians	50°-55°N	170°-175°W	198-1
Unimak Pass	50°-55°N	160°-165°W	197-1
Gulf of Alaska	55°-60°N	140°-145°W	195-3
Off Washington	45°-50°N	125°-130°W	157-4
Off Central California	35°-40°N	120°-125°W	121-3
Off Southern California	30°-35°N	115°-120°W	120-2
Off Central Mexico	20°-25°N	105°-110°W	83-2
Off El Salvador	10°-15°N	90°- 95°W	46-1
Off Colombia	0°- 5°N	80°- 85°W	9-1
Off Ecuador	0°- 5°S	80°- 85°W	308-1

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[5] Monthly means of merchant ship injection surface temperatures made by the Pacific Environmental Group, NMFS, Monterey, CA 93940. Means by 5-degree squares are means of four submeans by 1-degree squares to reduce spatial bias effects. Data of 1931-71 are from Marine Deck (TDF-11), National Climatic Center, EDIS, Asheville, NC 28801, and data 1972-79 are from weather reports received by Fleet Numerical Oceanography Center, Monterey, CA 93940.

[6] Local climatological data. National Climatic Center, EDIS, Asheville, NC 28801.

REGIONAL CONDITIONS

Eastern Bering Sea

Surface Pressure - Persistence of a deep Aleutian low surface atmospheric pressure system south of the Alaska Peninsula during winter 1977-78 resulted in strong easterly winds over the eastern Bering Sea during January, February, and even March 1978. Winds weakened in the spring transition period, becoming southeasterly during April and northeasterly during May. A major shift to westerly wind velocity components occurred in June with generally southwesterly summer winds shifting to weak westerly winds by September. The Aleutian low reformed at the normal time, in October, over the Gulf of Alaska, but its center was shifted slightly westward towards the Bristol Bay area, bringing strong easterly to northeasterly winds over much of the Bering Sea coast. The low shifted far into the western Bering Sea in November, and remained there through January 1979, bringing anomalous warming with the associated strong, persistent, moist southwesterly winds contrasting markedly with the cool, dry continental easterlies of the previous year. In February 1979 the low divided into a split system which brought a return of easterly winds reminiscent of conditions in early 1978.

Ice - The extent of ice cover in winter and the timing of the ice breakup in spring can be determined from infrared images from orbiting satellites. Weekly charts of ice distribution issued by the U.S. Navy and the National Environmental Satellite Service, NOAA, provide information on ice conditions in the eastern Bering Sea. A graphical representation of the mid-month positions of the ice edge for the ice seasons of 1977-78 and 1978-79 is shown in Figure 9. For comparison, the position of maximum ice extent during the previous season (April 1977) is also shown.

Overall, the trend of decreasing ice cover observed in recent years continued, progressing from above normal ice cover in 1976 to below normal coverage in 1979. Some differences in ice development were evident compared to last year. The very rapid northward retreat of the ice edge in late spring (May-June) 1978 was followed by a very slow ice advance in autumn 1978. This was apparent in the one-month delay, November vs. December, in the southward advance of ice through Bering Strait to St. Lawrence Island. In addition to the delay, the December 1978 ice extent was much less than in 1977, and similar conditions persisted through January 1979. An abrupt advance of the ice edge occurred in February 1979 when it attained the same position as in February 1978. However, in Bristol Bay the seaward extent of ice exceeded that of the entire previous year even though it was apparently short-lived.

Temperature - Air temperatures over the eastern Bering Sea reflected the warming trend observed since 1977. Whereas unusually cold conditions had occurred during the period 1971-76, with two pairs of adjacent severe winters (1970-71, 1971-72 and 1974-75, 1975-76), recent conditions have been unusually warm. The warm conditions resulted from the predominantly southerly geostrophic winds observed over the area during much of the year. Large positive anomalies occurred in late 1978 and particularly in early 1979 due to the early shift of the center of the Aleutian low to the west and its persistence there for several months. At St. Paul Island, Pribilof Islands, air temperatures (Fig. 7) were above normal in all but four months during January 1977-May 1979 and 2.0°C or more above normal in 15 out of the 29 months of the period. The year 1979 will apparently be very warm on the average as air temperatures during January-May at St. Paul were 3.4°-4.7°C

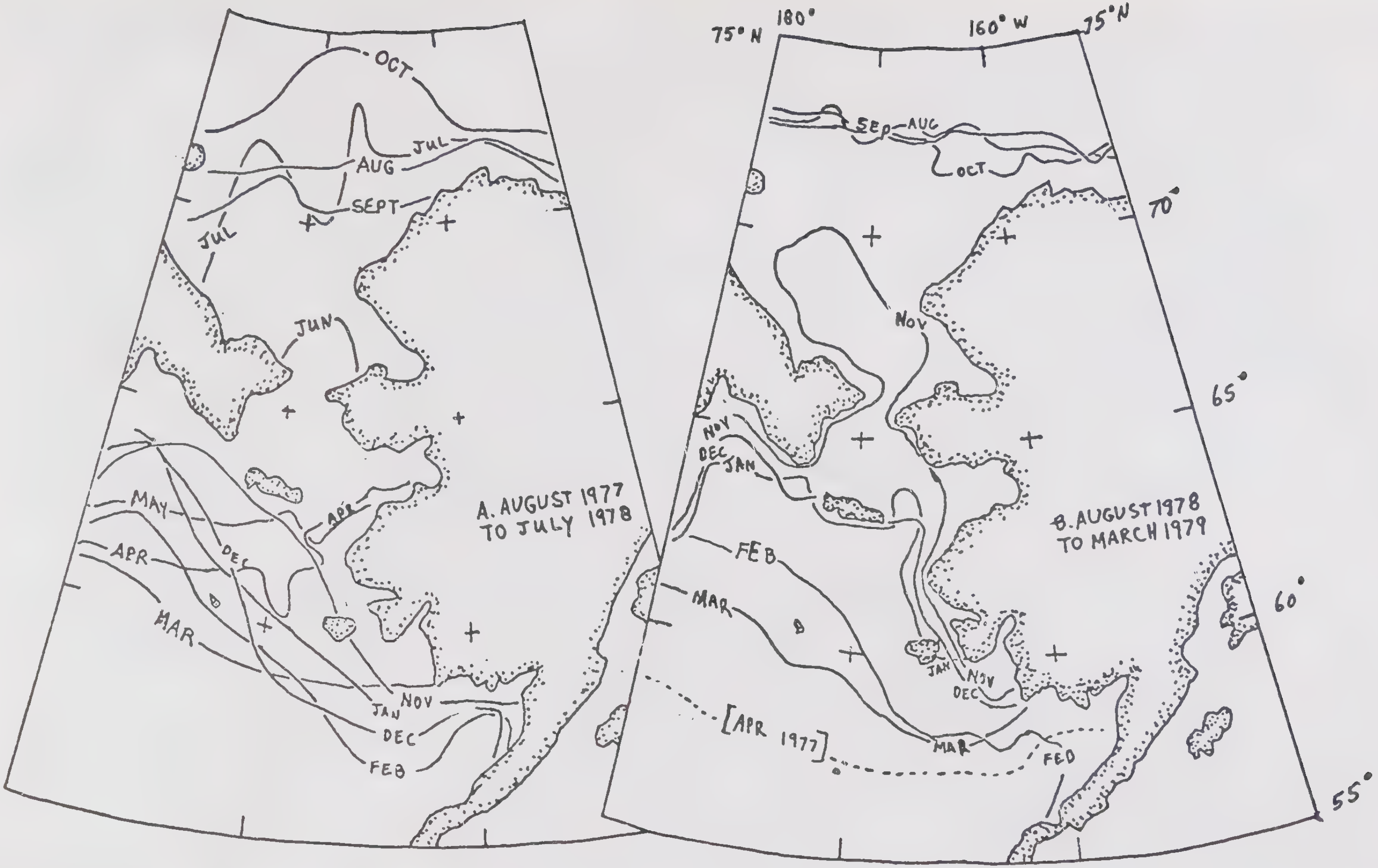
75° N
180°
160° W
75° N
70°
65°
60°
55°
A. AUGUST 1977 TO JULY 1978
B. AUGUST 1978 TO MARCH 1979
OCT
JUL
AUG
SEPT
JUL
JUN
MAY
APR
DEC
MAR
APR
JAN
NOV
DEC
FEB
SEP
AUG
OCT
NOV
NOV
DEC
JAN
FEB
MAR
JAN
NOV
DEC
[APR 1977]
MAR
FEB

Figure 9.--Midmonth locations of the ice front in the eastern Bering and Chukchi Seas during August 1977-March 1979, and, for comparison, April 1977. Plotted from data of the National Environmental Satellite Service and from ice cover analyses from the U.S. Naval Polar Oceanography Center, Suitland, MD 20393.

above normal.

Sea surface temperature data from the area show trends similar to the air temperatures. At square 197-1 (Fig. 7) SST's were above normal during most months of the period June 1977-March 1979, although in contrast to the St. Paul air temperatures, SST's were warmest in 1977 and more moderate, but still above normal during 1978 and early 1979.

Bottom temperatures from the area did not show as clear a trend. Bottom temperatures in 1978 indicated the outer shelf area near the Pribilof Islands to be about 1°C warmer than in 1977 and the inner shelf area (near 57°30'N, 163°W) to be about 1°-2C° colder than in 1977. Although data for 1979 are not yet available, the extent and general wind conditions indicated that the bottom temperatures in 1979 will be anomalously warm and similar to 1978.

The timing and location of herring spawning in Bristol Bay may be related to water temperatures and ice conditions.[7] Cold conditions that existed in spring 1976 were associated with a shift of some herring spawning from the north shore to the south shore of Bristol Bay. Warm conditions in early 1979 caused herring spawning to be up to two weeks early, commencing in mid-April along the north shore of the bay.

Northward shifts in the distribution of herring and shrimp may also occur over the shelf near the Pribilof Islands in response to mild temperature conditions. In an area near the Pribilofs normally fished by foreign trawlers in winter, a survey by the Northwest and Alaska Fisheries Center in March 1978 found only trace quantities of herring. The absence of herring was explained by a northward shift in the distribution of stocks associated with warm water temperatures.[8] A similar survey for shrimp in June and early July 1978 in the same region found only low shrimp concentrations in regions of normally significant abundance. Relatively high catches were made only along the northwest edge of the survey area.[9]

Other species were probably affected by the recent mild conditions as well. Straty and Jaenicke[10] found faster growth rates of juvenile Bristol Bay sockeye salmon in a warm year, 1967, than a cold year, 1971. Possibly mortality of sockeye due to predation was higher in 1971 than 1967 due to the slower growth rates. Also cold conditions in 1971 and 1972 may have caused the 1971 seaward migrants to remain an extra year at sea. Warm conditions in recent years thus may result in rapid growth and low mortality of sockeye. The recent mild conditions may also result in stronger year classes of various flounders (such as yellowfin sole, rock sole, flathead sole, and Alaska plaice).[11]

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[7] Reported on page 25 of the Monthly Report for April 1979, Northwest and Alaska Fisheries Center, NMFS, Seattle, WA 98112.

[8] Reported on page 27 of the Monthly Report for March 1978, Northwest and Alaska Fisheries Center, NMFS, Seattle, WA 98112.

[9] Reported on page 25 of the Monthly Report for July 1978, Northwest and Alaska Fisheries Center, NMFS, Seattle, WA 98112.

[10] Straty, R. R., and H. W. Jaenicke. Estuarine influence of salinity, temperature, and food on the behavior, growth, and dynamics of Bristol Bay sockeye salmon. Unpublished manuscript. Northwest and Alaska Fisheries Center, NMFS, Seattle, WA 98112.

[11] Reported on pages 25-27 of the Monthly Report for March, 1978, Northwest and Alaska Fisheries Center, NMFS, Seattle, WA 98112.

Pacific cod and Alaska pollock move onto the inner continental shelf in the eastern Bering Sea in summer months. During cold years, however, this movement is normally much less than during years with warmer temperatures (see footnote 11). Recent mild conditions would probably increase this inshore migration.

Runoff - The discharge of both the Yukon and Kuskokwim Rivers (Fig. 10) has a strong seasonal cycle with maximum discharge in summer (peaking in June) due to snow and ice melt, and minimum discharge in winter due to freezeup of the watersheds. The pulse of summer discharge has been below normal in recent years, particularly during 1974, 1976, and 1978. Although numerical data are not yet available for winter 1978-79, discharge during this period is reportedly about 10% greater than the previous year. Discharge of the Kvichak River, which is much more persistent in time than that of the Yukon or Kuskokwim Rivers due to the stabilizing effects of lakes in the watershed, was also below normal in 1974, 1976, and 1978.

Aleutian Islands to Icy Bay

Ice - Ice conditions in Prince William Sound and Cook Inlet were mild in both winters 1977-78 and 1978-79, and most bays were ice free by March of each year.

Temperature - Anomalies of sea surface temperatures along the southwest coast of Alaska are presented as time-distance matrices in Figure 11. In Marsden 5° square 197-1 (Fig. 7) south of the Peninsula, SST's had been below normal during 1971 to 1976 with the exception of fall 1974. Temperatures became anomalously warm in summer and fall 1977 and have been more nearly normal since then. Farther east at the head of the Gulf of Alaska (square 195-3, Fig. 7) SST's were generally similar, but were slightly below normal in 1978 and 1979.

During January-May 1978 SST's from Unimak Pass to Kodiak Island (Fig. 11) were above normal, became below normal during summer and early fall 1978, and were mixed the remainder of the period. SST's off Prince William Sound were colder than normal throughout 1978 and early 1979 as indicated at square 195-3.

Although historical bottom temperature data are sparse for this area, it is possible to compare bottom temperature regimes for the mid-shelf (about 50-150 m depth) near Kodiak Island for the period late winter-early spring for three consecutive years: 1976, 1977, and 1978 (using data collected on OSCEAP cruises) and also during the cold year 1972 (from a NWAFC cruise). Bottom temperatures of about 2°C occurred off Kodiak Island in May 1972, whereas mid-shelf temperatures in 1976, 1977, and 1978 were 2°-3°C warmer (3.7°C, 5.7°C, and 4.5°C, respectively). It is interesting to note that during the warm year, 1977, the permanent subsurface 5°C temperature maximum at about 250 m, associated with warm westward advection in the Alaskan Stream just seaward of the shelf break, was not clearly discernible for the first time.

Runoff - Several rivers flow into Cook Inlet, and the resulting dilute surface water flows southwestward through Shelikof Strait, north of Afognak and Kodiak Islands. However, the major river discharge at the head of the Gulf of Alaska is from the Copper River. Like the Yukon and Kuskokwim, the Copper River has a strong seasonal cycle with minimum discharge in winter and maximum discharge in summer, peaking in July (Fig. 10). At the time of this writing, data were available only through September 1978 and indicated above normal discharge in 1978.

Salinity - Further information on the surface salinity minima area reported last year for 1977 (McLain et al. 1979) is now available for late

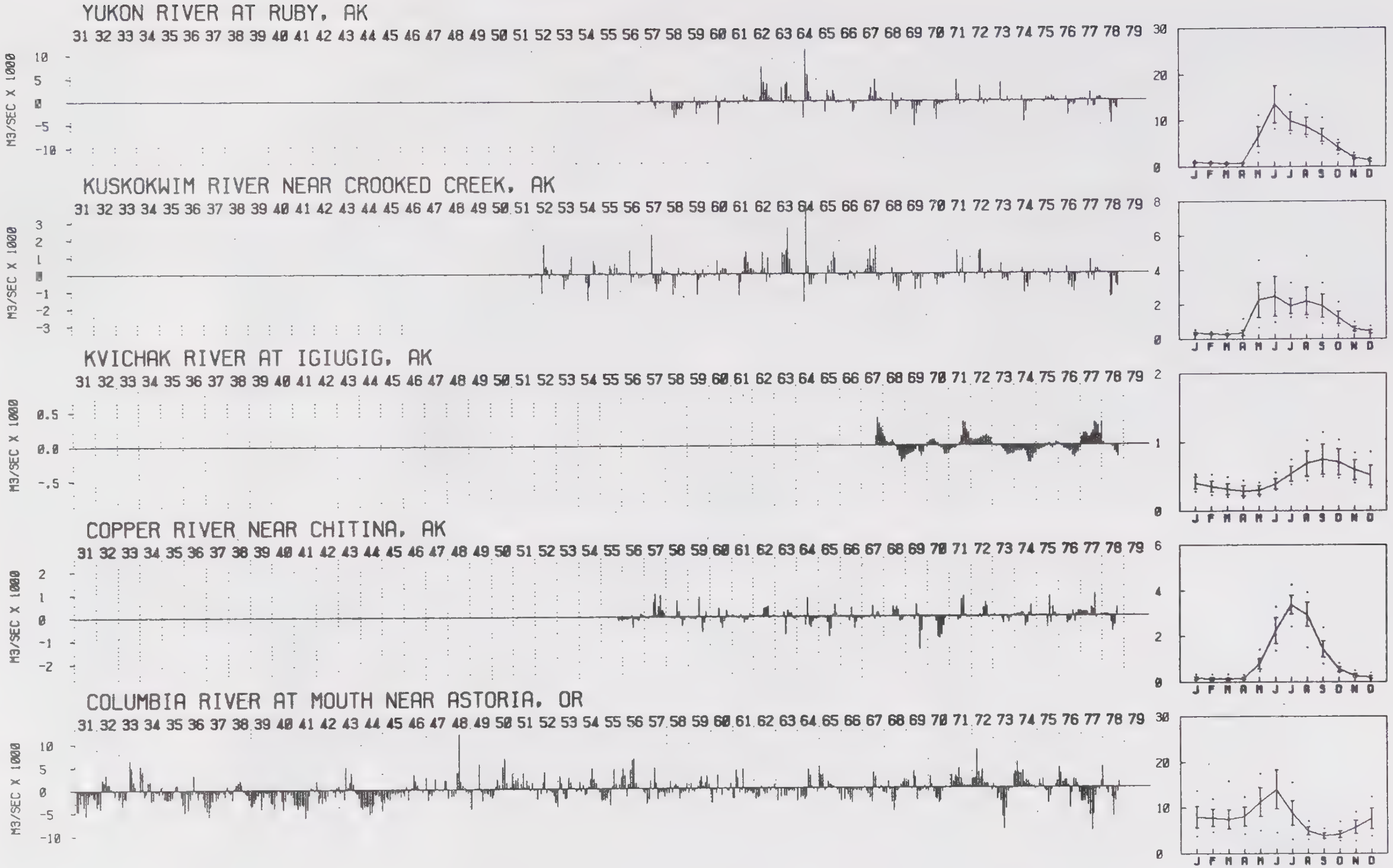
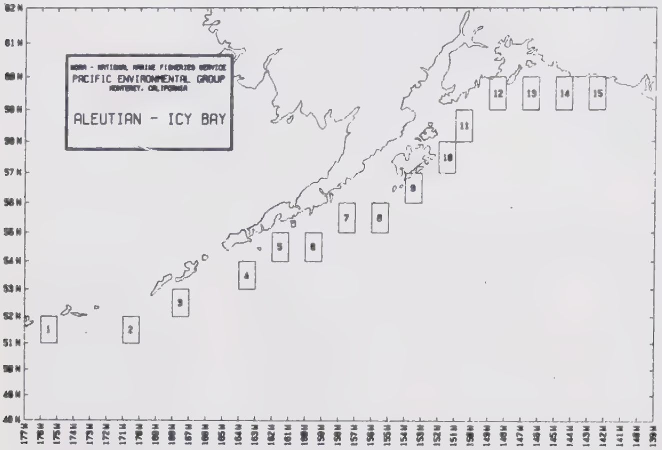
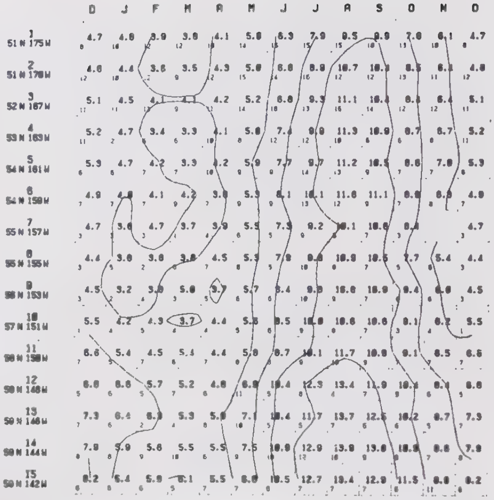


Figure 10.--Time series for 1931-79 of anomaly of river discharge into the ocean in thousands of cubic meters per second from the long-term mean reference period 1948-78. This is a different reference period than the 1948-67 period used in the remainder of the text to allow computation of a mean for the Kvichak River for which data start in 1967. Data from U.S. Geogological Survey. Data for Columbia River are extrapolated to the mouth of the river from observations upstream.





	D	J	F	M	A	M	J	J	A	S	O	N	D
1 51N 175W	4.7 8	4.0 10	3.9 12	3.0 12	4.1 10	5.0 14	6.3 15	7.9 15	8.5 15	8.9 10	7.0 13	6.1 10	4.7 8
2 51N 170W	4.0 12	4.4 10	3.6 12	3.5 9	4.3 12	5.0 15	6.0 14	8.9 10	10.7 12	10.0 12	8.5 13	6.0 11	4.0 12
3 52N 167W	5.1 11	4.5 11	4.1 12	4.1 9	4.2 12	5.2 14	6.0 10	9.3 13	11.1 16	10.0 14	8.0 12	6.4 12	5.1 11
4 53N 163W	5.2 11	4.7 2	3.4 8	3.3 6	4.1 10	5.0 8	7.4 12	9.0 12	11.3 10	10.9 8	8.7 6	6.7 8	5.2 11
5 54N 161W	5.3 6	4.7 6	4.2 7	3.3 7	4.2 10	5.9 9	7.7 9	9.7 14	11.2 13	10.5 9	8.6 7	7.0 7	5.3 8
6 54N 159W	4.9 7	4.0 7	4.1 7	4.2 9	3.0 7	5.3 9	8.1 9	10.1 13	11.0 12	11.1 9	8.0 7	6.5 8	4.9 7
7 55N 157W	4.7 3	3.6 3	4.7 3	3.7 1	3.9 4	5.5 6	7.3 5	9.2 9	10.1 8	10.0 7	8.0 3		4.7 3
8 55N 155W	4.4 3	3.0 5	3.0 2	3.0 6	4.5 7	5.3 8	7.0 5	9.0 10	10.0 6	10.5 7	7.7 5	5.4 6	4.4 3
9 56N 153W	4.5 3	3.2 2	3.0 4	5.0 3	3.7 5	5.7 6	8.4 6	9.0 10	10.0 9	10.9 7	9.4 6	6.0 6	4.5 3
10 57N 151W	5.5 1	4.2 4	4.3 5	3.7 4	4.4 4	5.5 9	8.5 6	10.0 9	10.6 0	10.6 7	9.1 3	6.2 4	5.5 1
11 58N 150W	6.6 7	5.4 5	4.5 7	5.4 6	4.4 7	5.0 8	8.7 8	10.1 9	11.7 10	10.0 9	9.1 7	8.5 7	6.6 7
12 59N 148W	6.0 5	6.6 6	5.7 5	5.2 7	4.0 6	6.9 11	10.4 5	12.3 8	13.4 4	11.9 7	10.4 9	8.0 6	6.0 5
13 59N 146W	7.3 7	6.4 6	6.0 2	5.3 4	5.0 8	7.1 10	10.4 5	11.7 5	13.7 7	12.5 6	10.2 6	8.7 5	7.3 7
14 59N 144W	7.0 8	5.9 6	5.6 9	5.5 10	5.5 6	7.5 9	10.0 10	12.9 12	13.0 10	13.0 9	10.0 8	8.0 7	7.0 8
15 59N 142W	6.2 6	5.4 8	5.9 6	6.1 5	5.5 7	8.0 7	10.5 8	12.7 7	13.4 7	12.0 7	11.5 8	8.0 11	6.2 8

SEA SURFACE TEMPERATURE LONG TERM MEAN 1971-1978

	1978												1979		
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
1 51N 175W	-.5 3	-.2 4	0.6 3	0.1 2	-.0 5	0.7 2	-1.0 5	0.5 1		-.3 2	-.1 2	0.0 1	-1.4 2	1.1 1	-.0 1
2 51N 170W		0.6 2	0.1 3	1.2 2	0.5 10	0.6 3	-1.1 4	0.3 2	1.7 1				-.4 2	0.5 1	
3 52N 167W		1.1 2	-.6 2	1.5 5	0.6 4	1.5 3	-2.3 1	-1.4 2		1.0 1				-.1 1	0.4 1
4 53N 163W	-.9 1	-.1 4	0.0 2	-.2 2	-.5 7	2.1 1	1.1 2	-1.0 3	0.3 2		1.6 3		-.9 1	-.4 1	
5 54N 161W	0.2 13	0.6 10	1.3 20	-.1 23	-.0 51	0.1 7	-1.0 13	-.2 6	0.7 5	0.2 3	0.5 9	-.3 1	0.1 5	-1.0 5	1.0 13
6 54N 159W	0.1 12	-.1 14	-.0 21	0.5 60	-.1 42	-1.5 11	-.9 21	-1.1 4	-.5 6	-1.3 4	1.5 5	2.0 5	1.0 6	-1.0 5	-.0 12
7 55N 157W	2.1 1	-.3 4	0.7 8	0.4 16	-.1 41	-.6 33	0.7 4	0.7 1	-.3 2				2.0 2	2.5	
8 55N 155W	-.0 5	0.0 46	1.7 2	0.6 5	1.5 2	-.3 12	-.9 1	-.2 4	-.7 2	1.0 3	1.1 5	1.0 1	0.9 2	0.2 1	1.2 3
9 56N 153W	1.0 20	-.1 4	-.1 5	0.0 8	0.4 11	-.5 43	-1.1 12	0.5 2	0.5 5	-.5 5	0.9 12		0.9 5	-.3 2	
10 57N 151W	0.2 76	0.0 128	0.4 101	-.1 147	-.1 9	-.2 16	-1.6 12	-.7 31	-2.3 64	-2.3 88	-1.0 126	-1.3 140	-.5 74	0.2 3	0.0 4
11 58N 150W	0.2 2	-.2 17	-.0 7	0.3 5	0.3 14	-.7 12	0.0 9	0.9 3	-.2 1	-.7 5	0.6 8	-1.0 1	-2.1 1	-.4 4	-.5 5
12 59N 148W		-1.0 3			-1.2 3	-.0 5	-.9 2							-1.7 3	
13 59N 146W	-1.5 8		0.0 1	-2.6 1	0.1 2	-.1 2			-.0 1			-2.3 1			
14 59N 144W	-1.0 8	-1.3 5	0.0 1	0.7 5	-2.0 13	-2.4 7	-1.7 4	-.0 6	-2.4 2	-1.0 6	-2.0 8	-1.7 4	-1.1 7	-1.2 5	
15 59N 142W	0.7 1				-1.0 1		-1.5 2	-.3 2							

Figure 11.--Time-space matrix for January 1978-March 1979 of anomaly of sea-surface temperature (lower) in degrees Celsius from the long-term mean reference period 1948-67 for a line of 1-degree squares along the coast from the Aleutian Islands to Ice Bay (locations shown in upper left). The long-term mean temperature values are shown in upper right and are based on data from the National Climatic Center, EDIS, Asheville, NC 28801.

summer 1978.[12] A marked seaward penetration of a low-salinity (31.6^o/oo) plume from the Copper River area (Fig. 12) extending 80 km south of the shelf break well into the oceanic regime of high-salinity (>32.6^o/oo) water was discovered. The seaward terminus of the plume reflected an anomalous eastward movement near the origin of the westward flowing boundary current, the Alaskan Stream. It is now evident that two sources of dilution, the Copper River in the northern Gulf and a tongue of low-salinity water from in the eastern Gulf, can contribute on a year-round basis to an anomalous offshore salinity minima area east of Kodiak Island (Ingraham 1979). Thus considerable complexity in surface flow is implied by the surface salinity distributions of 1977 and 1978. This may have considerable influence on the variability of the transport of ichthyoplankton, particularly halibut larvae, as well as on the seaward migration path of salmon smolts from southeast Alaska, British Columbia, Washington, and Oregon.

Icy Bay to Strait of Juan de Fuca

Temperature - Sea-surface temperatures along the coast of southeast Alaska and British Columbia (square 157-4; Fig. 7) were below normal from mid-1970 until mid-1976 (except for fall 1974), warmer than normal during early 1977 and early 1978, and colder than normal in early 1979. SST's plotted as time-distance matrices (Fig. 13) reflected the same pattern in 1978 but in greater detail: warmer than normal in early 1978, mixed until October, and colder than normal during November 1978-March 1979 (particularly at the southern end of the area off Vancouver Island).

Related bottom temperature data are sparse, but Douglas and Wickett (1978) found bottom temperatures up to about 2^{o}C above normal off Vancouver Island during a groundfish survey in early March 1978. SST's at that time and location were about 0.8^{o}C above normal (Fig. 13).

Surface and subsurface temperature data in the inside passages of southeastern Alaska during winter are available for the last three years from expendable bathythermograph (XBT) observations at 13 stations from Dixon Entrance northwards to Juneau.[13] Temperatures at the southern stations of the series are normally higher both at the surface (Fig. 14a) and at 90 m depth (Fig. 14b) than those at the northern stations. This is consistent with past SST's taken at Coast Guard lighthouses during the period 1959-74. Monthly mean SST data are not available from the lighthouses for the 1977-79 period; however, the 1979 XBT surface temperature observations are in the lowest 20 of observations from other available SST data sources for late January-early February. The cooling trend of the past two years is reflected in the late winter temperatures taken at 90 m at the 13 stations where the 1977 temperatures averaged 0.7^{o}C higher than those in 1978 and the 1979 temperatures averaged 1.5^{o}C lower.

Salinity - Measurements of surface salinity were made off the coast from Icy Bay to southeastern Alaska during summer 1977 by the Polish research vessel, Professor Siedlecki, and during summer 1978 by the NOAA research vessels, Miller Freeman and Oceanographer. The distributions of surface

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[12] Cruise No. 78-03, RV Miller Freeman, Northwest and Alaska Fisheries Center, NMFS, Seattle, WA 98112.

[13] XBT observations made from RV John N. Cobb and provided by R. R. Straty, Northwest and Alaska Fisheries Center, NMFS, Auke Bay, AK 99821.

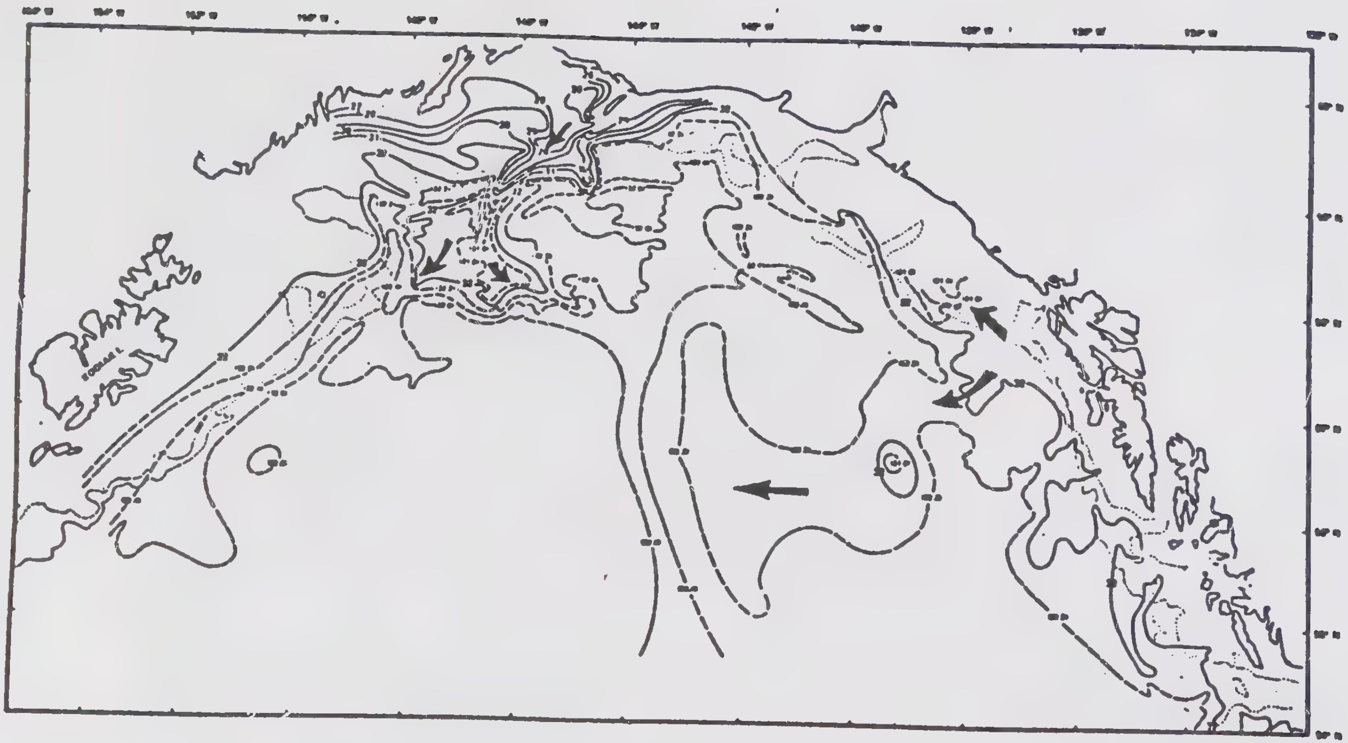
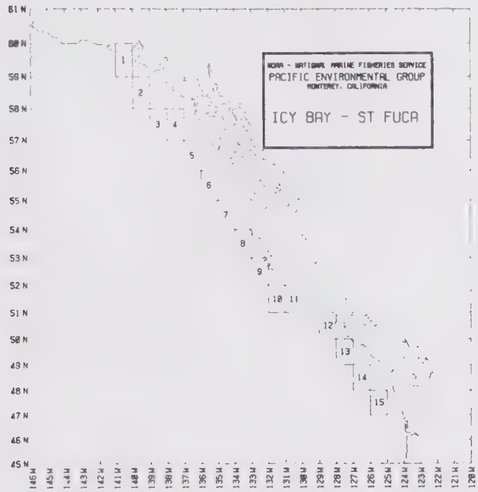


Figure 12.--Surface salinity in parts per thousand for summer 1978. Data were obtained from the NOAA research vessel (RV) *Miller Freeman*, the University of Alaska RV *Acona*, the Korean RV *Oh Dae San*, and the NOAA RV *Oceanographer*.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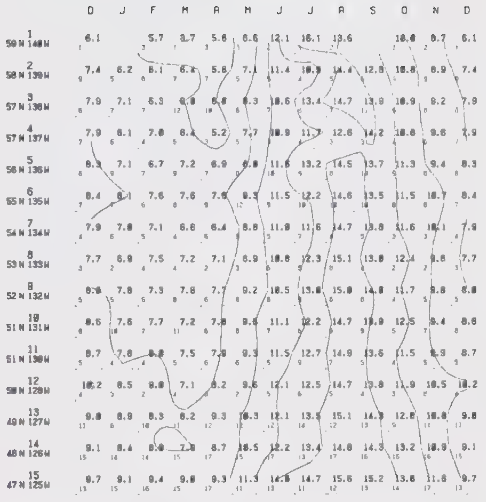

SEA SURFACE TEMPERATURE LONG TERM MEAN 1971-1978

	1978												1979		
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
1 59 N 140 W															
2 58 N 139 W	0.1 6				0.8 1	-.3 2	2.1 1	-1.6 1	0.6 1						-1.5 5
3 57 N 138 W	-1.0 1	-1.3 1					0.4 1					-1.2 1			
4 57 N 137 W	-.2 3				-2.3 3	0.1 3	0.8 2		0.2 1						
5 56 N 136 W		-.5 2			2.0 4	-1.1 1				-1.1 1					-1.2 1
6 55 N 135 W	-.9 1	-.5 2				-1.0 2									-1.3 2
7 54 N 134 W	1.9 1	0.1 4	-.2 3	1.6 1		0.1 1	0.8 1	-1.4 2			0.5 1	-.9 1	-.1 2		
8 53 N 133 W	2.1 1	-2.0 2	1.1 2	0.7 3	-1.2 1		0.3 5	-1.2 4	0.4 1	1.0 1		-.1 3	-.7 2	-.7 3	-1.0 2
9 52 N 132 W	-.3 5	0.1 8	-.1 4	1.3 4	-.9 7	1.0 5	-.3 13	-1.1 7	-.7 3	0.1 7	0.9 6	0.1 6	-.9 5	0.1 7	-1.6 4
10 51 N 131 W	0.9 3	-1.0 2	1.0 11	0.2 16	-.2 8	-.6 5	1.1 11	-1.5 4	-.5 1	-1.0 7	0.7 7	0.3 9	-.4 5	-1.1 11	-.1 5
11 51 N 130 W	0.4 2	0.1 7	1.2 2	1.3 10	0.8 9	0.7 7	-.2 8	-.5 6	0.0 6	1.0 2	0.1 5	-.2 4	-.6 3	-2.3 4	-.4 10
12 50 N 128 W	0.2 6	-1.4 6	1.1 4	1.1 9	1.0 5		0.4 7	-1.6 2	0.1 2	0.2 8	0.6 2	-3.0 1	-.5 1		0.4 4
13 49 N 127 W	0.2 12	-.3 10	0.8 14	0.1 12	0.9 18	-1.1 4	-2.1 6	-.9 2	0.1 3	-.1 10	-1.0 5	-.1 4	-1.7 15	-1.4 8	-.5 12
14 48 N 126 W	1.5 7	-.2 4	-.2 14	0.3 3	1.1 19	0.9 10	0.0 4	0.6 29	0.0 5	1.0 3	0.2 4	0.3 11	-1.3 10	-1.2 3	-.0 7
15 47 N 125 W	-1.4 3	-.3 8	0.4 5	0.8 5	0.7 16	0.6 60	-.9 74	-.2 7	0.3 6	1.7 2	-2.5 2	-1.1 2	-1.4 5	-1.9 8	0.5 14

Figure 13.--Time-space matrix for January 1978-March 1979 of anomaly of sea-surface temperature (lower) in degrees Celsius from the long-term mean reference period 1948-67 for a line of 1-degree squares along the coast from Icy Bay to the Strait of Juan de Fuca (locations shown in upper left). The long-term mean temperature values are shown in upper right and are based on data from the National Climatic Center, EDIS, Asheville, NC 28801.

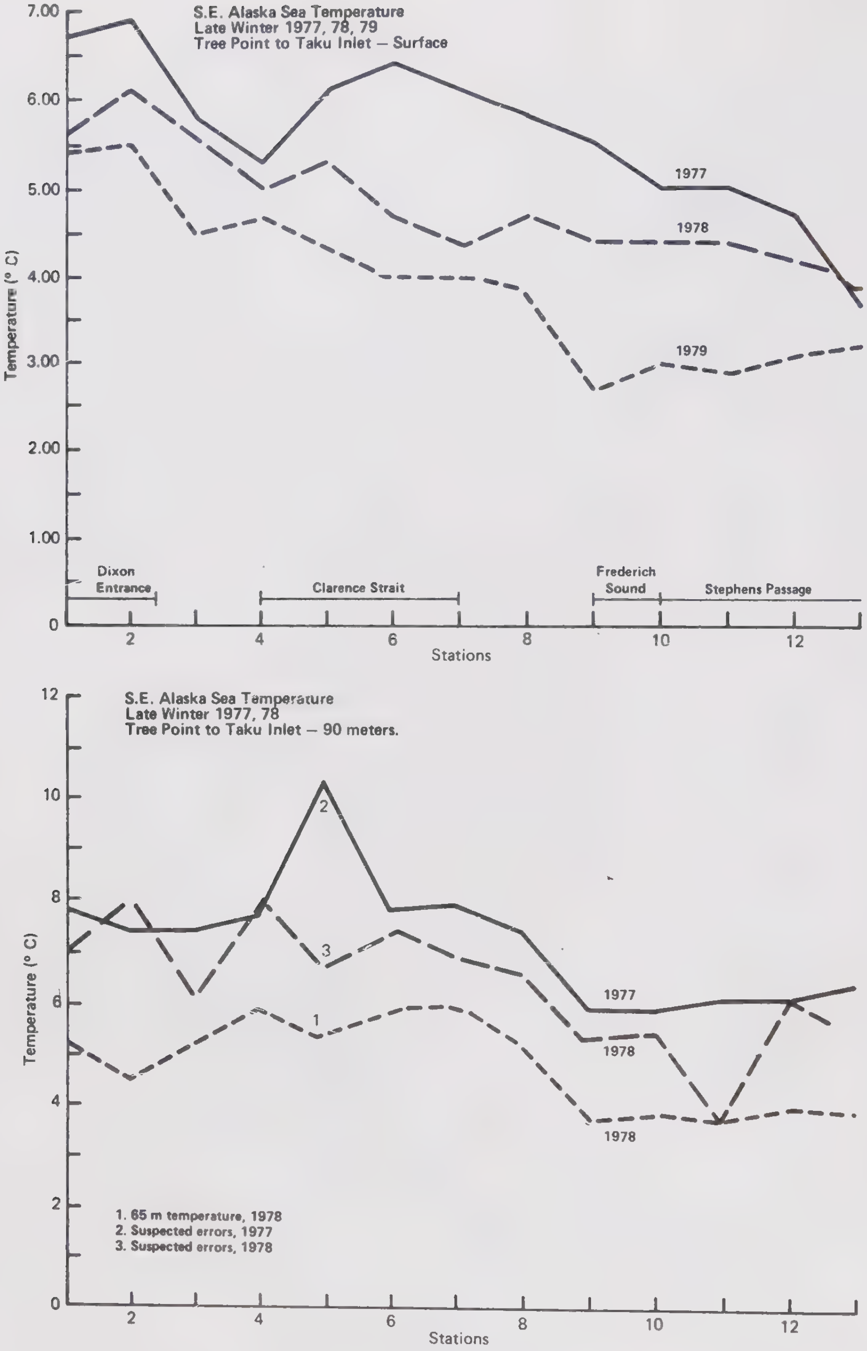

Figure 14.--a. Sea-surface temperature in degrees Celsius for late winter 1977, 1978, and 1979 from Tree Point to Taku Inlet, Alaska (upper).

b. Temperature at 90 m in degrees Celsius for late winter 1977 and 1978, and at 65 m depth in 1978 from Tree Point to Taku Inlet (lower).

Figures supplied by J. Ingraham, Northwest Fisheries Center, NMFS, Seattle, WA 98112.

salinity indicated that, north of 58°N, the trend of the isohalines was northwesterly and parallel to the shoreline, apparently reflecting longshore processes in the absence of major freshwater sources. South of 58°N tongues of dilute water (<32.0°/oo) extended about 100 km seaward near local sources of runoff. The major feature, reported for the first time in 1977 and again evident in 1978, was the bifurcation in coastal flow near 58°N. This bifurcation was evident as a tongue of low-salinity (<32.0°/oo) water pointing toward the northwest in 1977, but in 1978 the major tongue had a salinity of about 0.2°/oo higher and the axis of the tongue trended more perpendicular to shore in a westward to southwestward direction (Fig. 12). Near 55°N a wide band of water with a salinity less than 32.4°/oo suggested that the extent of the major effects of coastal dilution was about 100 km farther seaward in 1978 (142°W). True oceanic salinities of 32.6°/oo were not encountered until nearly mid-Gulf (about 144°W) during both years.

Coastal Circulation - As has been mentioned, in late 1977 and early 1978 onshore Ekman transport was stronger and more toward the northeast than normal along the coast of southeastern Alaska and British Columbia. As a result, the northward flow of the Gulf of Alaska Gyre was intensified and SST's were above normal. Douglas and Wickett (1978) attributed the above normal bottom temperatures off Vancouver Island in early 1978 to stronger than normal onshore Ekman transport of warm surface waters from the southwest with convergence and sinking of surface water at the coast.

Numerous unusual biological events were observed in the area, although their relation to the onshore transport is as yet poorly understood. These included failure of the acorn barnacle, Balanus cariosus, to settle during its normal winter settling season; accentuated settlement and growth of two other barnacle species during the winter months (both of these species usually are most vigorous during a July-October interval); accentuated algal growth on the shore (diatoms especially, but also Ulva and Nereocystis); a massive incursion, on shore, of salps in unheard of quantity; numerous comments by fishermen of blue sharks in very close to shore and in unusual abundance; and finally, unusually few Japanese glass floats coming ashore.[14]

Reports from salmon trollers[15] confirm the massive intrusion of salps off southeastern Alaska in summer 1978 and also the occurrence then of saury and sea turtles (leatherbacks). Both of the latter species normally occur in offshore waters to the south and thus may have been transported to coastal waters of southwestern Alaska by anomalous northward, onshore transport. Wickett[16] suggested that "the early strong Ekman transport to the northeast is associated with the unprecedented large percentage (70) of adult Fraser River sockeye that returned to the river through Queen Charlotte Strait instead of using the Straits of Juan de Fuca." Part of the mechanism is believed to be a northern displacement of a plume of low-salinity water from

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[14] These observations were made by Dr. R. T. Paine and his graduate students of the Department of Zoology, University of Washington, Seattle, WA 98195, at a site near the tip of the Olympic Peninsula in Washington and at Glacier Bay, Alaska (Lasker 1978).

[15] B. L. Wing, Northwest and Alaska Fisheries Center, NMFS, Auke Bay, AK 99821. Personal communication.

[16] P. Wickett. Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada. Personal communication.

Queen Charlotte Sound (cf. Fig. 12). The herring roe fishery in Barkley Sound just inshore of the survey area reported on by Douglas and Wickett (1978) was disrupted by the unusual behaviour of the fish which spawned at greater than normal depths."

Adult pink salmon returns to Little Port Walter Bay, Baranof Island, in southeastern Alaska in 1978 had an unusually high ocean survival (Herd 1979). However, this was probably more related to conditions in 1977 when salmon fry entered the ocean than in 1978 when the adults returned.

Strait of Juan de Fuca to Gulf of California

Temperature - Anomalies of sea-surface temperature along the west coast of the United States had somewhat similar trends as in areas to the north. At square 121-3 (Fig. 7) off central California, SST's have been below normal almost continuously since mid-1970 with short above normal periods in mid-1977 and early 1978. At squares 120-2 off southern California and 83-2 off the Gulf of California, the basic pattern of variation was similar to that at square 121-3 except that it was shifted to slightly more positive anomalies. Thus at squares 120-2 and 83-2, SST's were below normal in early 1971 and 1972 and again in 1973 and 1975, above normal in late 1976 and early 1978, and near normal values in late 1979.

Figures 15 and 16 give more details on SST variations along the coast during 1978 and early 1979. Along the California coast, north of Point Conception (34°-40°N; Fig. 15) SST's were anomalously warm during early 1978 during the period of extreme low upwelling, but fell to below normal levels in June. Farther north (41°-48°N) the above normal SST's persisted until November when anomalous cooling became evident. SST's were uniformly below normal during winter 1978-79 and the anomalies were generally negative by 1°-2°C. By March 1979 SST's returned to normal values.

Along the coast of southern California and Baja California (Fig. 16), the fluctuations of SST were similar to those observed to the north. Above normal SST's occurred in early 1978 and persisted until summer and early fall when anomalous cooling occurred. SST's were below normal off Baja California in fall and into winter 1978-79, but were again near normal in March 1979.

Runoff - Maximum mean monthly runoff of the Columbia River[17] into the ocean normally occurs in June and minimum discharge normally occurs in September. However, the seasonal variation of runoff can vary markedly from year to year. For example, in 1977 minimum monthly mean discharge occurred in July (McLain et al. 1979) and the maximum (roughly four times the minimum) occurred in December. These variations were caused by drought during most of 1977 and heavy precipitation in winter 1977-78.

Conditions in 1978 indicated a return to more normal trends with some exceptions. Above normal runoff continued through March 1978 (Fig. 10). The maximum discharge occurred in May 1978, rather than June, and the June discharge was nearly 50 less than normal.

Coastal Circulation - During January-March 1978 southerly winds occurred over California during anomalous high pressure and drought conditions. As has been mentioned, upwelling during this period was extremely low (Fig. 5)

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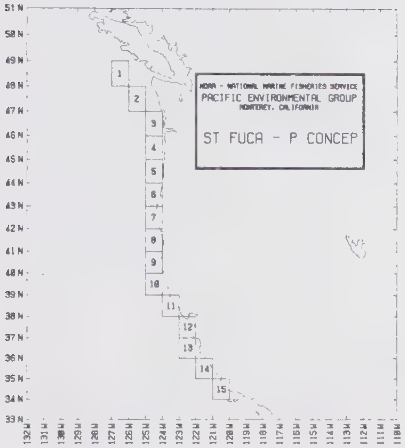
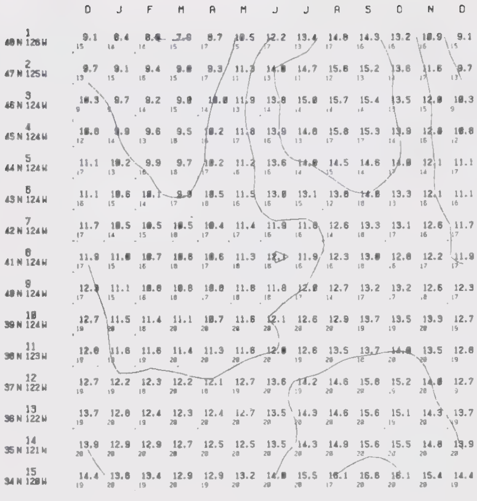
[17] S. F. Kapustka, U.S. Geological Survey, Portland, OR 92708. Personal communication.



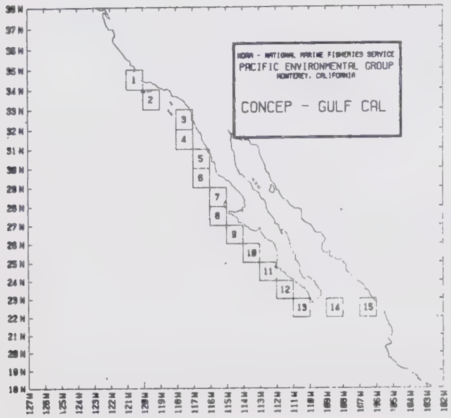


	D	J	F	M	A	M	J	J	A	S	O	N	D
1 48 N 126 W	9.1 15	8.4 14	8.0 14	7.8 15	8.7 17	10.5 15	12.2 17	13.4 13	14.8 17	14.3 16	13.2 16	10.9 16	9.1 15
2 47 N 125 W	9.7 13	9.1 15	9.4 16	9.0 15	9.3 17	11.3 11	14.0 13	14.7 11	15.6 12	15.2 13	13.6 14	11.6 17	9.7 13
3 46 N 124 W	10.3 9	8.7 9	9.2 14	9.0 15	10.0 14	11.9 13	13.8 14	15.0 14	15.7 14	15.4 14	13.5 13	12.0 15	10.3 9
4 45 N 124 W	10.0 12	9.9 14	9.6 13	9.5 18	10.2 16	11.8 17	13.9 16	14.0 13	15.8 17	15.3 17	13.9 14	12.0 16	10.0 12
5 44 N 124 W	11.1 17	10.2 13	9.9 16	9.7 18	10.2 17	11.2 16	13.6 16	14.0 14	14.5 15	14.6 14	14.0 17	12.1 14	11.1 17
6 43 N 124 W	11.1 16	10.6 15	10.1 14	9.8 17	10.5 18	11.5 16	13.0 16	13.1 15	13.0 12	14.0 18	13.3 13	12.1 16	11.1 16
7 42 N 124 W	11.7 17	10.5 14	10.5 15	10.5 18	10.4 17	11.4 17	11.9 16	11.8 16	12.6 14	13.3 18	13.1 17	12.6 16	11.7 17
8 41 N 124 W	11.9 17	11.0 15	10.7 16	10.8 18	10.6 17	11.3 18	12.1 18	11.9 16	12.3 16	13.0 18	12.0 16	12.2 17	11.9 17
9 40 N 124 W	12.0 17	11.1 15	10.0 16	10.8 18	10.0 17	11.8 18	11.8 18	12.0 17	12.7 14	13.2 17	13.2 17	12.6 18	12.3 17
10 39 N 124 W	12.7 19	11.5 20	11.4 18	11.1 20	10.7 20	11.6 20	12.1 20	12.6 20	12.9 20	13.7 19	13.5 19	13.9 20	12.7 15
11 38 N 123 W	12.0 19	11.6 19	11.8 19	11.4 20	11.3 20	11.6 20	12.0 20	12.8 19	13.5 20	13.7 18	14.0 20	13.5 20	12.0 19
12 37 N 122 W	12.7 19	12.2 19	12.3 18	12.2 20	12.1 18	12.7 19	13.6 20	14.2 19	14.6 20	15.0 20	15.2 15	14.0 20	12.7 9
13 36 N 122 W	13.7 19	12.8 20	12.4 19	12.3 20	12.4 20	12.7 20	13.5 20	14.3 20	14.6 20	15.6 20	15.1 15	14.3 20	13.7 19
14 35 N 121 W	13.9 20	12.9 20	12.9 20	12.7 20	12.5 20	12.5 20	13.5 20	14.3 20	14.9 20	15.6 22	15.5 20	14.8 20	13.9 20
15 34 N 120 W	14.4 19	13.6 20	13.4 19	12.9 20	12.9 19	13.2 20	14.0 20	15.5 20	16.1 17	16.8 20	16.1 20	15.4 20	14.4 19

SEA SURFACE TEMPERATURE LONG TERM MEAN 1971-1978

	1978												1979		
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
1 48 N 126 W	1.5 7	-.2 4	-.2 14	0.3 3	1.1 10	0.9 10	0.0 4	0.6 29	0.0 5	1.0 3	0.2 4	0.3 11	-1.3 10	-1.2 3	-.0 7
2 47 N 125 W	-1.4 3	-.3 8	0.4 5	0.8 5	0.7 16	0.6 60	-.9 74	-.2 7	0.3 6	1.7 2	-2.5 2	-1.1 2	-1.4 5	-1.9 6	0.5 14
3 46 N 124 W	0.2 220	0.6 240	0.6 253	-.3 229	-.5 16	2.2 13	-.7 173	-1.0 35	-.3 152	0.7 170	-.4 168	-.3 205	-2.0 120	-2.4 203	-.8 249
4 45 N 124 W	0.3 5	0.7 8	1.4 5	0.7 10	0.5 7	1.9 110	0.2 54	0.1 12	0.9 14	1.4 17	-1.5 6	-1.4 4	-1.0 1	-1.2 3	0.4 6
5 44 N 124 W	0.5 5	1.5 11	2.0 6	1.3 6	0.7 13	1.6 218	-.5 170	0.2 76	0.9 36	1.4 23	0.2 10	-.6 4	-1.4 8		1.0 10
6 43 N 124 W	0.3 3	1.1 13	1.9 8	0.7 3	0.4 5	1.3 89	0.5 118	0.9 105	2.0 47	1.2 8	-.7 2	-2.0 6	-1.2 7	-1.0 3	-.6 11
7 42 N 124 W	1.5 3	0.8 5	0.7 5	0.6 8	1.0 4	2.1 27	1.1 27	0.1 9	2.2 3	-1.4 1	-.1 6	-.5 3	-.5 7	-2.0 9	-.9 6
8 41 N 124 W	0.5 4	0.4 10	2.0 7	0.8 12	1.3 5	1.1 127	0.4 153	1.4 6	2.0 6	1.7 2	2.6 11	-1.9 5	-1.5 5	-2.0 4	-.2 19
9 40 N 124 W	1.0 6	1.7 11	1.5 7	1.3 13	0.9 12	0.7 50	-.3 47	0.2 9	0.0 3	1.5 6	-.4 13	-2.1 10	-.4 8	-1.0 5	0.6 19
10 39 N 124 W	0.7 11	1.2 17	1.4 6	1.6 21	0.3 13	-.1 10	0.5 7	0.5 10	0.4 7	-.5 8	-1.5 14	-2.3 14	-.7 12	-1.4 10	0.3 31
11 38 N 123 W	1.3 6	1.2 8	0.4 4	1.2 10	-.1 9	-.2 14	-.2 7	0.6 12	0.8 6	0.1 6	-1.5 9	-1.5 12	-.7 4	-.9 6	0.1 26
12 37 N 122 W	1.4 2	0.1 8	0.2 4	1.3 7	-.5 5	-1.1 2	-1.8 2	0.8 5	-1.6 5	0.1 2	0.2 3	-.6 5	-.4 6	-2.0 3	-1.3 8
13 36 N 122 W	0.5 9	0.6 14	1.3 10	0.9 10	-.5 18	-1.6 13	-1.1 25	0.6 12	-.7 9	0.4 5	-1.6 13	-1.9 35	-1.0 13	-1.6 7	0.1 24
14 35 N 121 W	0.8 12	0.7 15	1.5 17	0.7 16	-.4 19	-1.0 7	0.5 14	-.8 10	-1.4 14	-1.4 5	-.5 13	-.9 11	-1.1 15	-1.1 14	0.3 15
15 34 N 120 W	2.0 4	-1.5 5	2.0 8	-.3 6	0.4 12	-1.6 5	-2.4 8	-.4 7	-.9 5	1.1 3	0.4 9	-.3 7	-1.2 8	-.4 4	-.9 8

Figure 15.--Time-space matrix for January 1978-March 1979 of anomaly of sea-surface temperature (lower) in degrees Celsius from the long-term mean reference period 1948-67 for a line of 1-degree squares along the coast from the Strait of Juan de Fuca to Point Conception (locations shown in upper left). The long-term mean temperature values are shown in upper right and are based on data from the National Climatic Center, EDIS, Asheville, NC 22801.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PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
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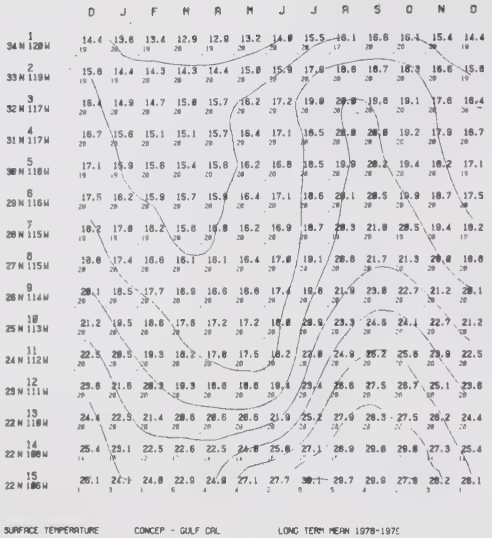

	D	J	F	M	A	M	J	J	A	S	O	N	D
1 34 N 120 W	14.4 19	13.6 20	13.4 19	12.9 20	12.9 19	13.2 20	14.0 20	15.5 20	16.1 17	16.6 20	16.1 20	15.4 20	14.4 19
2 33 N 119 W	15.0 19	14.4 19	14.3 20	14.3 20	14.4 20	15.0 20	15.9 20	17.0 20	18.6 20	18.7 20	18.3 20	16.6 20	15.0 19
3 32 N 117 W	16.4 20	14.9 20	14.7 20	15.0 20	15.7 20	16.2 20	17.2 20	19.0 20	20.0 20	19.8 20	19.1 20	17.6 20	16.4 20
4 31 N 117 W	16.7 20	15.6 20	15.1 20	15.1 20	15.7 20	16.4 20	17.1 20	18.5 20	20.0 20	20.0 20	19.2 20	17.9 20	16.7 20
5 30 N 116 W	17.1 19	15.9 19	15.6 20	15.4 20	15.8 20	16.2 20	16.8 20	18.5 20	19.9 20	20.2 20	19.4 20	18.2 20	17.1 19
6 29 N 116 W	17.5 20	16.2 20	15.9 20	15.7 20	15.9 20	16.4 20	17.1 20	18.6 20	20.1 20	20.5 20	19.9 20	18.7 20	17.5 20
7 28 N 115 W	18.2 19	17.0 19	16.2 19	15.8 20	16.0 20	16.2 20	16.9 20	18.7 20	20.3 19	21.0 20	20.5 19	19.4 20	18.2 19
8 27 N 115 W	18.8 20	17.4 20	16.6 20	16.1 20	16.1 20	16.4 20	17.0 20	19.1 20	20.8 20	21.7 20	21.3 20	20.0 20	18.8 20
9 26 N 114 W	20.1 20	18.5 20	17.7 20	16.9 20	16.6 20	16.8 20	17.4 20	18.8 20	21.9 20	23.0 20	22.7 20	21.2 20	20.1 20
10 25 N 113 W	21.2 20	19.5 20	18.6 20	17.8 20	17.2 20	17.2 20	18.0 20	20.9 20	23.3 20	24.6 20	24.1 20	22.7 20	21.2 20
11 24 N 112 W	22.5 20	20.5 20	19.3 20	18.2 20	17.8 20	17.5 20	18.2 20	22.0 20	24.9 20	26.2 20	25.6 20	23.9 20	22.5 20
12 23 N 111 W	23.6 20	21.6 20	20.3 20	19.3 20	18.8 20	18.6 20	19.4 20	23.4 20	26.6 20	27.5 20	26.7 20	25.1 20	23.6 20
13 22 N 110 W	24.4 20	22.5 20	21.4 20	20.6 20	20.6 20	20.6 20	21.9 20	25.2 20	27.9 20	28.3 20	27.5 20	26.2 20	24.4 20
14 22 N 108 W	25.4 14	23.1 14	22.5 12	22.6 [illegible]	22.5 14	24.0 14	25.0 [illegible]	27.1 [illegible]	28.9 [illegible]	28.8	29.0	27.3 14	25.4 14
15 22 N 106 W	26.1 1	24.1 3	24.8 1	22.9 6	24.8 4	27.1 4	27.7 2	30.1 6	29.7 5	29.9 4	27.9	26.2 3	26.1 1

SEA SURFACE TEMPERATURE CONCEP - GULF CAL LONG TERM MEAN 1978-1979

	1978												1979		
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
1 34 N 120 W	2.0 3	-1.5 5	2.0 8	-.3 6	0.4 12	-1.6 9	-2.4 8	-.4 7	-.9 5	1.1 3	0.4 9	-.3 7	-1.2 8	-.4 4	-.9 8
2 33 N 119 W	1.0 6	0.7 2	-.1 5	-.7 3	-.6 2	-.9 5	-.1 3	0.2 1	1.3 1	-.8 3	-1.0 16	-1.2 3	-2.4 3	-.6 3	-.5 5
3 32 N 117 W	1.7 5	1.2 10	2.4 17	1.8 50	0.3 9	1.6 13	-.2 5	1.2 13	0.1 8	1.4 10	0.8 22	-1.2 9	-.2 20	-.4 9	0.3 33
4 31 N 117 W	1.3 7	1.3 11	0.6 3	1.1 9	0.7 6	0.4 6	0.5 3	0.2 7	-.0 4	0.1 7	-.4 8	0.0 9	-.2 13	-.4 10	0.1 11
5 30 N 116 W	1.0 3	0.4 5	0.7 8	1.2 15	1.0 15	1.0 4	-.2 3	0.1 6	-1.7 3	-.4	0.2 13	-1.4 10	-.3 8	-.6 11	0.1 14
6 29 N 116 W	1.7 10	1.2 15	1.8 14	0.5 24	0.9 21	0.9 10	0.5 7	-.2 10	-1.1 5	0.5 16	0.6 13	-.3 15	-.2 12	-.7 16	0.0 28
7 28 N 115 W	1.0 8	0.3 6	0.9 4	0.9 9	0.7 18	0.2 5	-1.7 5	0.5 6	-1.3 9	-.7 3	-.1 7	-1.7 8	-1.0 11	-.8 9	0.3 12
8 27 N 115 W	0.3 9	1.0 13	1.7 11	0.3 14	0.4 24	1.4 11	0.2 11	-.5 11	-1.5 10	0.4 10	0.4 12	-.4 15	-1.0 10	-1.4 9	-.1 13
9 26 N 114 W	1.9 15	0.4 11	1.2 12	1.1 25	0.8 28	0.2 13	0.1 16	-1.0 15	-2.0 6	0.1 16	-.0 13	-1.1 14	-1.0 18	-1.5 12	0.2 17
10 25 N 113 W	1.6 10	1.1 20	1.1 14	0.6 21	1.4 12	-1.0 10	-1.0 10	-.9 10	-2.0 13	-.4 8	-.4 17	-1.5 9	-1.0 14	-.8 14	-.2 16
11 24 N 112 W	1.2 13	0.5 10	1.7 12	0.4 20	0.9 18	1.0 14	1.0 12	0.6 13	-1.4 5	-1.0 14	-1.5 13	-1.2 16	-.5 10	-1.0 14	-.2 12
12 23 N 111 W	0.9 8	0.9 13	0.4 8	0.8 20	0.3 20	0.4 10	1.0 10	1.3 21	-.9 12	0.5 8	0.7 13	-1.9 7	-1.4 18	-1.2 11	0.1 17
13 22 N 110 W	1.7 8	1.5 12	0.6 11	-.0 14	0.1 18	0.5 9	-.4 16	0.4 13	-1.3 9	0.7 10	0.2 16	-1.7 6	-.7 17	-1.3 14	-.4 17
14 22 N 108 W	0.9 1	0.5 1	-.6 1	0.3 3	0.2 4	-1.2 5	0.9 3		0.7 6	0.6 7	1.0 2	-1.1 26	-1.3 14	-1.0 38	-1.4 9
15 22 N 106 W		0.0 1									-.5 2	-2.3 3		-2.0 2	-.6 4

Figure 16.--Time-space matrix for January 1978-March 1979 of anomaly of sea-surface temperature (lower) in degrees Celsius from the long-term mean reference period 1948-67 for a line of 1-degree squares along the coast from Point Conception to the Gulf of California (locations shown in upper left). The long-term mean temperature values are shown in upper right and are based on data from the National Climatic Center, EDIS, Asheville, NC 28801.

and the opposite circulation, downwelling, occurred. Ekman transports at points off California (Fig. 2) were also weaker than long-term mean conditions during this period. Sea-surface temperatures were up to 2°C above normal during December-April. These conditions were associated with apparently stronger than normal transports by the northward flowing, near shore California Counter Current (Davidson Current).

The effects of increased northward transport by the California Counter Current on marine populations remain unclear. Parrish and Bakun (1979) suggested that the extremely low upwelling indices during early 1978, together with associated warmer than normal SST's, could have allowed anomalous northward migration of southern species along the coast. Commercial swordfish landings in 1978 in southern California were nearly double the previous record (set in 1978) and may have resulted from increased northward advection.

Anomalously strong northward advection along the coast, combined with above normal SST's, may also explain unusual recoveries of tagged billfish off southern California in October 1978.[18] Of the several thousand marlin tagged by the Southwest Fisheries Center, all those previously recovered had been taken to the south and southwest of San Diego, off Baja California and central Mexico, around the Hawaiian Islands, and near the Marquesas Islands in the southeast Pacific. None before had ever been recovered off southern California.

Other unusual occurrences of tropical species were reported in summer 1978. A triggerfish (a tropical reef fish) was caught near Monterey, CA, on September 20, 1978.[19] Radovich (1960) discussed anomalous catches of various species, including triggerfish, along the California coast during the unusual warm period in 1957 and 1958.

The onshore Ekman transport in early 1978 appeared to concentrate anchovy larvae near shore and allow improved reproductive success. Seckel et al. (1978) described the large-scale atmospheric circulation over the west coast during the period 1976-78 and the upwelling conditions that resulted from that circulation. They suggested that onshore Ekman transport during early 1978 (and the resulting weak upwelling indices) apparently concentrated anchovy larvae and their forage organisms near the California coast and resulted in good spawning success relative to the spawning stock size. In other years when onshore transport is less apparent, spawning success may be reduced by loss of larvae to offshore areas. Seckel et al. further suggested that the large numbers of young-of-the-year anchovy observed in southern California waters during spring and summer 1978 and unusually large concentrations of young fish as far north as Monterey Bay appear to support their hypothesis.

Salinity - Salinities along the California coast were below normal during 1978 and early 1979, particularly in the first quarter of each year. Data on temperature and salinity at the surface and bottom (about 5 m) at Scripps Pier in La Jolla, CA, are shown in Figure 16. The origin of the low-salinity water is unclear; it may be due to such processes as increased advection of low-salinity water from northern areas, above normal precipitation, or decreased upwelling of high-salinity water from depth. Low-salinity water was also observed off southern California in 1978 during CalCOFI cruises,[20] and was noted up to 1,500 km offshore of central California in surface salinity observations made by merchant ships.[21]

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[18] News release, October 17, 1978, Southwest Fisheries Center, NMFS, La Jolla, CA 92038. Two record recoveries made of tagged billfish off southern California.

[19] Monterey Peninsula Herald, September 20, 1978.

The time series of salinity at Scripps Pier in 1978-79 looks remarkably similar to that observed during the period 1941-42 (Fig. 17). Note also the occurrence of above normal temperatures at Scripps Pier in the winters of 1976-77 and 1977-78, and the similar above normal temperatures in the winters of 1939-40 and 1940-41.

Eastern Tropical Pacific

An important process causing variations of oceanographic conditions in the Eastern Tropical Pacific (ETP) from one year to the next is the so-called El Niño. When this event occurs, sea levels and sea-surface temperatures are above normal in the waters off Ecuador and Peru, the normal upwelling of nutrient-rich deep waters into the surface waters is disturbed and biological productivity of the area is reduced. Wyrtki (1978) suggested that the El Niño conditions normally follow periods of strong trade winds which pile water up in the western tropical Pacific. As the trade winds relax, eastward flow increases in the Equatorial Counter Current towards South America, raising SST's and sea levels along the coast, depressing the thermocline, and reducing the normal upwelling of nutrient-rich water from depth.

Southern Oscillation - The variation of atmospheric pressure across the tropical Pacific, called the Southern Oscillation, has been correlated with recruitment of skipjack tunas (IATTC 1978, 1979). Quinn (1978, 1979) developed an index of the Southern Oscillation as the difference in surface atmospheric pressure between Easter Island in the eastern Pacific and Darwin, Australia, in the western Pacific:

$$\text{S.O. Index} = P_{\text{Easter}} - P_{\text{Darwin}}.$$

A time series of this index is shown in Figure 18 for the period January 1948-June 1979. During 1970-71 the index was positive for many months, indicating a strong pressure difference across the Pacific and strong trade winds. In 1972 the difference fell rapidly, the trade winds relaxed, and SST's (squares 308-1, 9-1, and 46-1 in Fig. 8) and sea levels (data for California stations shown in Fig. 6) increased as a major El Niño developed (Miller and Laurs 1975). In 1973 the pressure difference increased, sea levels and SST's returned to more normal values, and the El Niño condition disappeared. In 1975-76 a weaker cycle occurred with a positive pressure difference in 1975, a falling difference in 1976, and a weak El Niño response. The pressure difference has remained negative (near zero in mid-1978) since 1976 for an unusually long period of time. Thus the trade winds have been weak for the last three years and the probability of a major El Niño in 1979 and early 1980 is very low.

Temperature - Oceanographic conditions in the ETP are commonly monitored from patterns of SST and its anomaly from a long-term mean. Maps of anomaly of SST in the ETP are published monthly in Fishing Information. The following discussion is based on those maps, and the reader is referred to them and the accompanying descriptions for details

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[20] R. Lynn, Southwest Fisheries Center, NMFS, La Jolla, CA 92037. Personal communication.

[21] J. F. T. Saur, Scripps Institution of Oceanography, La Jolla, CA 92038. Personal communication.

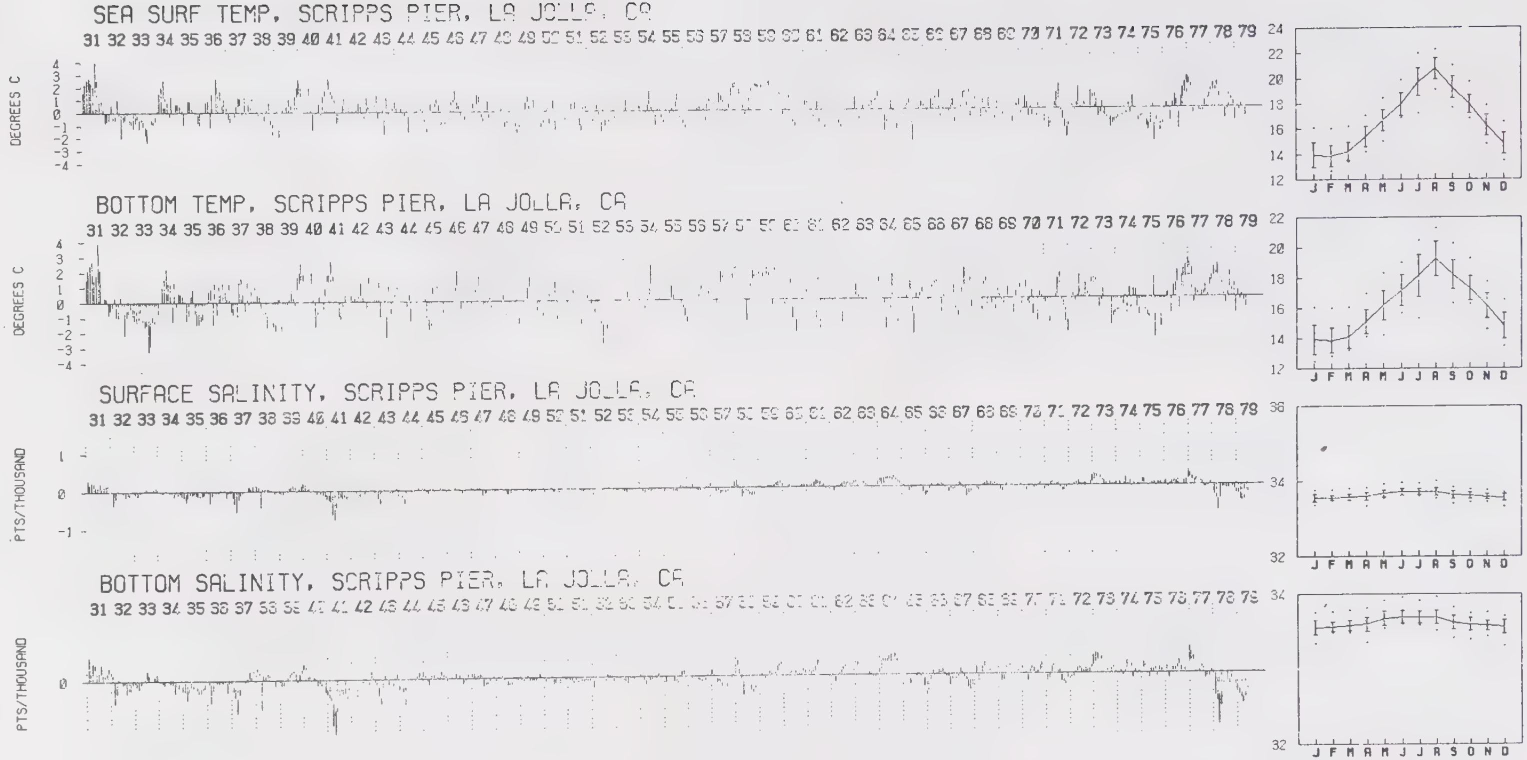

Figure 17.--Time series for 1931-79 of anomaly of temperature in degrees Celsius and salinity in parts per thousand at the surface and bottom (5 meters) at the end of Scripps Pier, La Jolla, CA, from the long-term mean reference period 1948-67. Data from C. Conway, Scripps Institution of Oceanography, La Jolla, CA 92038.

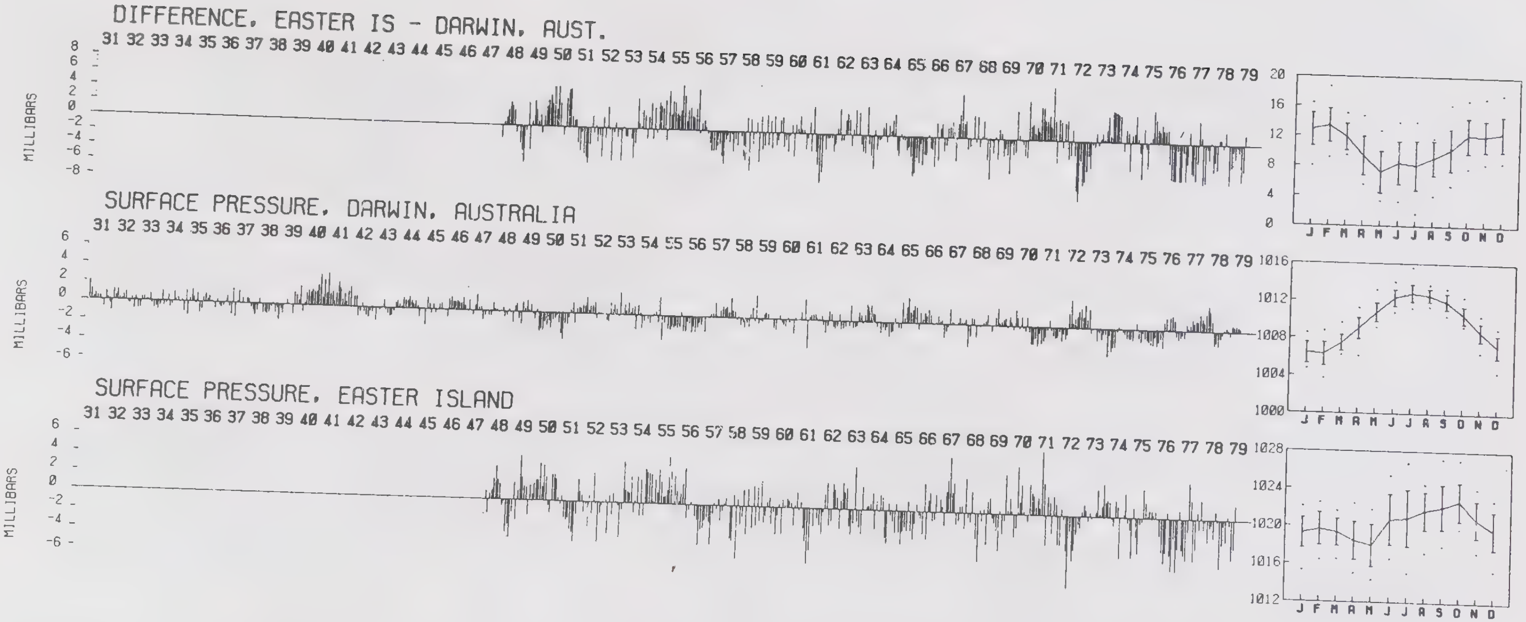

Figure 18.--Time series for 1931-79 of anomaly of surface atmospheric presure in millibars at Easter Island and Darwin, Australia, from the long-term mean reference period 1948-67. The difference between the two stations is an index of the Southern Oscillation. Developed by W. Quinn, Oregon State University, Corvallis, OR 97331.

of ocean conditions during 1978 and early 1979.

During January 1978 SST's were above normal over much of the ETP in the area west of 110°W due to weak trade winds and a relaxation of the subtropical high-pressure system off California. Upwelling off Peru and westward along the Equator caused below normal SST's east of 110°W as did strong wind mixing in the Gulfs of Tehuantepec and Panama and along the west coast of Nicaragua.

This general pattern persisted through February, but by March SST's had returned to near normal values over most of the area. Below normal SST's persisted in the Gulfs of Tehuantepec and Panama due to northerly winds blowing across Central America from the Gulf of Mexico.

In April the subtropical high-pressure system over the ETP continued weaker than normal. Lighter than normal winds and less than normal cloud cover resulted in above normal SST's in a large area southwest of Baja California. A dramatic increase in equatorial upwelling reduced SST's to below normal values in a broad band along the Equator from the coast of Peru to 180° and beyond.

Below normal SST's along the Equator continued as the dominant feature of the SST patterns from April through September. The colder than normal temperatures were typical of an "anti-El Niño" situation where the trade winds are moderately strong (note the positive pressure differences in mid-1978, Fig. 20) and upwelling of cold water along the Equator was intense.

The band of below normal SST's along the Equator broke up in fall, and by November SST's were near normal over the entire ETP, except for below normal SST regions along the equator near Equador, in the Gulf of Tehuantepec, and off Baja California. This general pattern of near normal SST's over the ETP with below normal SST pools near the coast persisted through March 1979.

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Improved Bounds for Aggregated Linear Programs

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A method of Kallio for improving bounds on the optimal value of a linear program calculated from an intermediate iteration is used to improve Zipkin's bounds for an aggregated linear program. Both theoretical and computational results are given, demonstrating the improvement due to these new bounds.

ONE METHOD for solving large scale linear programs (LPs) or large scale Markov decision processes (MDPs) is by first finding an exact solution to a smaller, aggregated problem; disaggregating this solution to the original problem; and finding bounds on the error from using the approximate solution. This has been studied extensively by Zipkin (1980) for fixed-weight aggregation.

In related work, Kallio (1977) derives bounds for a nonaggregated LP which is stopped at some iteration of the simplex method, and uses a decomposition technique and marginal analysis to tighten the bounds. For nonaggregated LPs, Kallio's Theorem 1 and Zipkin's Proposition 2 are identical. In this paper, Kallio's method is used to improve the bounds for aggregated LPs and for fixed-weight aggregated MDPs. The notation of this paper follows that of Zipkin whenever possible.

1. The Model

The original LP is

$$\begin{aligned} z^* = \max\ & cx \\ \text{subject to } & Ax \leq b \\ & x \geq 0 \end{aligned} \tag{1}$$

where $c = (c_j)$ is an n-vector, $b = (b_i)$ is an m-vector, $A = (a_{ij})$ is an $m \times n$ matrix, and $x = (x_j)$ is an n-vector of variables.

Let $\sigma = \{S_k{:}k = 1, \cdots, K\}$ be an arbitrary partition of $\{1, \cdots, n\}$, and

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$n_k = |S_k|$. Define $\mathscr{A}^k$ to be the submatrix of A consisting of those columns whose indices are in S_k. Define c^k and x^k similarly. Let g^k be a non-negative n_k-vector whose components sum to unity, and define:

$$\bar{A}^k = \mathscr{A}^k g^k,\ \bar{c}_k = c^k g^k,\ k = 1, \cdots, K.$$

Let $\bar{A} = (\bar{A}^1, \cdots, \bar{A}^K)$, $\bar{c} = (\bar{c}_1, \cdots, \bar{c}_K)$ and X a K-vector of variables. Then the weighted column aggregate problem of (1) is:

$$\begin{aligned} \bar{z} = \max\ & \bar{c}X \\ \text{subject to } & \bar{A}X \le b \\ & X \ge 0. \end{aligned} \tag{2}$$

Let z^* be the optimal value of (1) and let x^*, an n-vector, be an optimal solution to (1). Zipkin shows that for any partition $\sigma' = \{S_k' : k - 1, \cdots, K'\}$ of $\{1, \cdots, n\}$ such that there exist known positive numbers $\{d_1, \cdots, d_n\}$ and known non-negative numbers $\{p_1, \cdots, p_K\}$ with:

$$\textstyle\sum_{j \in S_k'} d_j x_j^* \le p_k,\ k = 1, \cdots, K' \tag{3}$$

then

$$\bar{z} \le z^* \le \bar{z} + \xi_a$$

where

$$\xi_a = \textstyle\sum_{k=1}^{K'} [\max_{j \in S_k'} \{(c_j - \bar{u}A^j)/d_j\}]^+ p_k,$$

$\bar{u}$ is the vector of optimal dual variables of (2), A^j is the jth column of A, and $(a)^+ = \max(0, a)$.

Kallio assumes there are two known n-vectors, l and p, $0 \le l \le p \le \infty$, such that if the constraint $l \le x \le p$ is added to (1), then the value of an optimal solution is unchanged. If $\bar{z}$ is the value of a current feasible basis, and $\bar{u}$ is the corresponding vector of simplex multipliers, Kallio's bounds are:

$$\bar{z} \le z^*\ \bar{u}b + \textstyle\sum_j (c_j - \bar{u}A^j)^+ \cdot p_j + \sum_j (C_j - \bar{u}A^j)^- \cdot l_j \tag{4}$$

where $(a)^- = \min(a, 0)$.

Kallio shows how a certain restricted dual problem can be solved by marginal analysis to yield a tighter bound than does (4). In what follows, it is assumed d_j in (3) is identically 1 for all j. The extension to the more general case is straightforward. Extending this idea to the aggregated LP, amend to (1) the K constraints $\sum_{j \in S_k} x_j \le p_k$, $k = 1, \cdots, K$. Then the dual to this restricted problem is

$$\begin{aligned} &\text{minimize } ub + \textstyle\sum_{k=1}^{K} \delta_k p_k \\ &\text{s.t. } \textstyle\sum_i a_{ij} u_i + \delta_k \ge c_j,\ j \in S_k;\ k = 1, \cdots, K,\ u \ge 0;\ \delta \ge 0. \end{aligned} \tag{5}$$

Let $\bar{c}_j = c_j - \bar{u}\bar{A}^j, \bar{\delta}_k = \max_{j \in S_k} (\bar{c}_j)^+$ and $\bar{\delta} = (\bar{\delta}_k)$. By assumption, (1) and (5) have the same optimal value z^*.

Lemma 1. *$(\bar{u}, \bar{\delta})$ is a feasible solution to* (2.5).

Lemma 1 leads to the extension of Kallio's Theorem 1 for an aggregated LP. Consider (5) with u restricted to the set $U = \{u \mid u = \theta\bar{u}, \theta \in R\}$. The new restricted dual program is

$$\begin{aligned} &\text{minimize } \bar{z}\theta + \textstyle\sum_{k=1}^{K} \delta_k p_k \\ &\text{s.t.} (\textstyle\sum_i a_{ij}\bar{u}_i)\theta + \delta_k \geq c_j, \qquad j \in S_k; j = 1, \cdots, n, \\ &\quad \bar{u} \geq 0; \delta_k \geq 0, \qquad k = 1, \cdots, K \end{aligned} \tag{6}$$

Let $z(\theta)$ be an optimal value of (6) as a function of θ.

Theorem 1. *$z(\theta)$ is a convex and piecewise linear function. Let $z_-(\theta)$ be the left-hand derivative of $z(\theta)$ with respect to θ. Then the possible discontinuity points of $z_-(\theta)$ where an optimum can occur are at $\theta_1, \cdots, \theta_n$ where:*

$$\theta_j = \begin{cases} c_j / \sum_i a_{ij}\bar{u}_i & \text{if } \sum_i a_{ij}\bar{u}_i \neq 0 \\ \infty & \text{if } \sum_i a_{ij}\bar{u}_i = 0, \quad \text{for all } j. \end{cases}$$

Proof. The dual LP (6) can be decomposed into K subproblems, each of which has a solution value $\max_{j \in S_k}(c_j - (\theta \sum_i a_{ij}\bar{u}_i))^+ p_k$, which are convex and piecewise linear. This implies that $z(\theta)$ is given by:

$$z(\theta) = \bar{z}\theta + \textstyle\sum_{k=1}^{K} [\max_{j \in S_k} (c_j - (\theta \sum_i a_{ij}\bar{u}_i))]^+ p_k$$

which is convex and piecewise linear since it is the sum of such functions. The rest of the theorem follows from this property and inspection of the formula for $z(\theta)$.

Let $z(\theta^*)$ be the minimum value of $z(\theta)$, that is an optimal solution to (6) over all possible values of θ.

Corollary 1. $\bar{z} \leq z^* \leq z(\theta^*) \leq \bar{z} + \xi_a$.

Proof. $z(\theta^*) \leq \bar{z} + \xi_a$ since $\bar{z} + \xi_a$ is equivalent to $z(1)$, and θ^* minimizes $z(\theta^*)$. By weak duality, a solution to (5) is greater than or equal to a solution of its dual problem. Since the constraint $u \in U$ restricts (5), $z(\theta^*)$ is no less than an optimal value to (5), hence $z(\theta^*)$ is a legitimate upper bound.

Following and extending Kallio, for any value of θ, define the index $j(\theta, k)$ to be the j where $(c_j - \theta \sum_i a_{ij}\bar{u}_i)$ is maximized for $j \in S_k$, $k = 1, \cdots, K$. Define the set $J(\theta) = \{j \mid j = j(\theta, k), k = 1, \cdots, K\}$, and define the set $I(\theta) = \{j \mid j \in J(\theta); \theta_j \leq \theta \text{ and } \sum_i a_{ij}\bar{u}_i < 0 \text{ or } \theta_j > \theta \text{ and } \sum_i a_{ij}\bar{u}_i \geq 0\}$. Then $z_-(\theta) = \bar{z} - \sum_{j \in I(\theta)} p_k(\sum_i a_{ij}\bar{u}_i)$. Using this formula for $z_-(\theta)$, the marginal analysis to find $z(\theta^*)$ proceeds as in Kallio. At θ^*, $z(\theta^*)$ can be evaluated by the formula $z(\theta^*) = \bar{z}\theta^* + \sum_{j\in I(\theta^*)} (c_j - \theta_i{}^* a_{ij}\vec{u}_i)p_k$. This involves evaluating at most K terms.

Examples. This example is from Zipkin. The original problem is:

$$\begin{aligned} z^* = {} & \max 2.5x_1 + 3x_2 + 4x_3 + 5x_4 \\ & \text{subject to } 4x_1 + 5x_2 + 7x_3 + 10x_4 \le 54 \\ & \qquad x_1 + 2x_2 + x_3 + 2x_4 \le 10 \\ & \qquad x_1, x_2, x_3, x_4 \ge 0. \end{aligned}$$

An optimal solution is $x_1{}^* = 16/3$, $x_3{}^* = 14/3$, $x_2{}^* = x_4{}^* = 0$, $z^* = 32$. Zipkin solves two aggregate problems. For the first, $K = 2$, $s_1 = \{1, 2\}$, $s_2 = \{3, 4\}$, the column weights in each partition are (0.5, 0.5). The second aggregate problem changes the column weights to (0.75, 0.25). For the first problem, $\bar{z} = 28\,5/6$, $\bar{u} = (21/48\ \ 25/48)$, and with $p_1 = 10$, $p_2 = 8$, the bounds are $28\,5/6 \le z^* \le 34\,11/24$. For finding the improved bound, $\theta_1 = 1.101$, $\theta_2 = 0.4290$; $\theta_3 = 2.116$, $\theta_4 = 0.9231$. Then $\theta^* = \theta_1 = 1.101$, and the improved bound is $28\,5/6 \le z^* \le 32.1855$.

For the second aggregate problem, Zipkin's bounds are $30\,2/7 \le z^* \le 33\,23/70$. For the improved bounds, $\theta_1 = 1.051$, $\theta_2 = 0.9817$; $\theta_3 = 1.0606$, $\theta_4 = 0.8794$. At an optimum, $\theta^* = \theta_1 = 1.051$, and the improved bound is $30\,2/7 \le z^* \le 32.1231$. In both problems, the improved upper bound is an extremely tight bound on the true optimal value z^*.

In Mendelssohn (1978a–c) these results are extended to derive improved bounds by dominance for aggregated MDPs. A numerical example is presented for a real life model that has been suggested for use in managing salmon runs.

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Managing Stochastic Multispecies Models*

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ABSTRACT

Qualitative properties of optimal policies for stochastic, multispecies harvesting models are described. Conditions that imply that a k-species model can be decomposed into k single species models are discussed. For a discrete, stochastic version of the Lotka-Volterra models, it is shown that finding an optimal policy can be narrowed to finding the globally optimal harvest, and to using constraints developed on the partial derivatives of an optimal policy to accelerate computations. For a discrete stochastic version of a competition model developed by Silliman, it is proven that knowledge of the globally optimal harvest is sufficient to completely describe an optimal policy. Approximate policies that are easier to solve are suggested. The results suggest that an optimal harvesting policy will tend to simplify the ecosystem—that is harvest to low levels unwanted or less valuable species.

INTRODUCTION

In a previous paper, I extended the results for stochastic, single-species, pooled-age-class harvesting models to stochastic multi-age-class models (see [4] and references cited there). These models consider a single stock or species separate from its interaction with other species. Biological systems are noted for having complex food webs, and it is desirable to examine the effects these interactions have on optimal harvesting strategies. This is particularly true when two or more interacting species are being exploited by a single fishery, or are being managed by a single controller or agency.

Let x_t (possibly a k-vector) denote the size of a stock or stocks at the beginning of period, t, z_t (possibly a k-vector) the amount harvested in period t, and $y_t = x_t - z_t$ the amount remaining at the end of period t after

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harvesting has ceased. Assume x_{t+1} is a random function of y_t, that is,

$$x_{t+1} = S[y_t, D_t],$$

where $D_1, D_2, \ldots, D_T$ are independent, identically distributed random vectors, distributed as the generic random vector D.

In each period, observing x and harvesting to y produces a return $G(x,y)$, discounted by a factor α, $0 < \alpha \leqslant 1$. Following Mendelssohn and Sobel [5], this problem can be formulated as the following system of recursive functions:

$$\begin{aligned} &f_0(\cdot) \equiv 0, \\ &f_n(x) = \max_{0 < y < x} \{J_n(x,y) : x \in X\}, \end{aligned} \tag{I}$$

where

$$J_n(x,y) = G(x,y) + \alpha E\{f_{n-1}(S[y,D])\}$$

and where the domain X is a convex set, representing the set of all possible population sizes. It is assumed that X is bounded, which is realistic, since real populations cannot be negative, nor can they be infinite.

Multispecies harvesting models have been considered to a limited extent in the literature. Quirk and Smith [6] present results for a continuous-time, deterministic Lotka-Volterra-type system, but under very restrictive assumptions. Hilborn [1] uses numerical dynamic programming to study harvesting strategies for noninteracting species that are jointly harvested.

Three types of stochastic multispecies models are analyzed in this paper. The first is a model of k noninteracting species that are jointly harvested, but whose return structure is separable. It is shown that the entire problem can be reduced to k one-dimensional problems. This result is similar to previous results in [4].

The second model is a discretized version of the Lotka-Volterra model for competing species or predator-prey systems. In this model, the growth rate for each species and all the interaction coefficients are assumed to be random variables. It is also assumed that each species is harvested, and that each species can be targeted. The first assumption can be easily relaxed; the second assumption can be relaxed if the model of "by-catches" retains all the necessary concavity properties. For example, if the by-catches are linear, then straightforward modifications to Theorem 2 can be made.

The third model is a model due to Silliman [9] based on laboratory experiments. This model is similar to the Lotka-Volterra equations, except that the interaction term is linear instead of quadratic.

1. MODELS AND RESULTS

The k-dimensional notation of Mendelssohn [4] is adapted to the k-species problem by letting superscript i denote species instead of age-class. The first model to be considered has k species that interact only in the return function. A single boat or fleet harvests k noninteracting species. Let $g^i(x^i,y^i)$ be the net benefit of harvesting species i from x^i individuals to y^i individuals. The boat or fleet may also experience costs that are independent of whether or not it harvests, but depend on the total time away from port. One possible structure for these costs is that it is proportional to a weighted sum of the total harvest sizes. This could arise if the time spent in searching for and harvesting each species is proportional to the size of the harvest from that species. Thus, the total return from harvesting is

$$G(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{k} \{ g^i(x^i,y^i) - cw^i(x^i - y^i) \}, \qquad (1)$$

$$c, w^i \geqslant 0 \qquad \text{for all } i.$$

The growth of each species is a random function which depends on the number of individuals of that species only, that is,

$$x^i_{t+1} = s^i[\mathbf{y}_t, \mathbf{d}_t] = s^i\left[y^i_t, d^i_t \right], \qquad i = 1, \ldots, k. \qquad (2)$$

Theorem 1 states that the model described by Eqs. (1) and (2) is separable into k subproblems where each species is considered separately from all others. The advantage of this is that a k-dimensional problem can be reduced to k one-dimensional problems where the stronger results of Mendelssohn and Sobel [5] can be applied.

THEOREM 1

In the dynamic-programming problem (I), *if* $G[\mathbf{x},\mathbf{y}]$ *and* $\mathbf{S}[\mathbf{y},\mathbf{d}]$ *are given by Eqs.* (1) *and* (2), *respectively, then the problem can be separated into k one-dimensional subproblems of the form*

$$f^i_0(\cdot) \equiv 0,$$
$$f^i_n(x^i) = \max_{0 < y^i < x^i} \{ g^i(x^i,y^i) - cw^i(x^i - y^i) + \alpha E f^i_{n-1}(s^i[y^i,d^i]) \}.$$

Proof. The proof follows from a similar proof in Veinott [10]. ■

The Lotka-Volterra equations are usually represented as

$$\frac{dx^i(t)}{dt} = r^i x^i(t) + x^i(t) \sum_j a_{ij} x^j(t), \qquad (3)$$

$$i,j = 1, \ldots, k, \qquad k = 2w.$$

If a_{ij} is positive, then species j is a prey of species i. If a_{ij} is negative, then species j is either a competitor or a predator of species i. (Detailed discussions of these equations and their shortcomings can be found in [3, 7, 8].)

One possible discretized version of (3) is

$$x_{t+\delta}^i - x_t^i = \delta x_t^i\left(r^i + \sum_{j=1}^{k} a_{ij}x_t^j\right), \qquad i,j=1,\ldots,k. \tag{4}$$

To include harvesting, it is assumed that a harvest of z_t^i from any species i produces a return $p^i z_t^i$ in period t, and that the transition (4) depends only on the number left after harvest, $y_t^i = x_t^i - z_t^i$. It is further assumed that each r^i, $i=1,\ldots,k$, and a_{ij}, $i,j=1,\ldots,k$, are random variables such that $r^i \geqslant 0$ with probability one, $a_{ij} \geqslant 0$ with probability one if species j is a prey of species i, and $a_{ij} \leqslant 0$ with probability one if species j is a predator or competitor of species i. The dynamic program then is

$$\begin{aligned} &f_0(\cdot) \equiv 0, \\ &f_n(\mathbf{x}) = \max_{0<\mathbf{y}<\mathbf{x}} \{J_n(\mathbf{x},\mathbf{y})\}, \end{aligned} \tag{5}$$

where

$$J_n(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{k} p^i(x^i - y^i) + \alpha E f_{n-1}(\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}])$$

and $\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}]$ is given by [4].

The analysis concentrates on a modification of (5). Let

$$G(\mathbf{y}) = \alpha E\left(\sum_{i=1}^{k} p^i s^i[\mathbf{y},\mathbf{r},\mathbf{a}]\right) - \sum_{i=1}^{k} p^i y^i. \tag{6}$$

Then, as in [4, Theorem 3], there is an equivalent problem:

$$\begin{aligned} &f_0(\cdot) \equiv 0, \\ &f_n(\mathbf{x}) = \max_{0<\mathbf{y}<\mathbf{x}} \{J_n(\mathbf{y})\}, \end{aligned} \tag{7}$$

where

$$J_n(\mathbf{y}) = G(\mathbf{y}) + \alpha E f_{n-1}(\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}])$$

and n goes from 1 to $T-1$ if the original planning horizon is T periods. Let $\mathbf{A}_n(\mathbf{x})$ be an optimal policy function with component function $a_n^i(\mathbf{x})$.

THEOREM 2

Let $\mathbf{x}_n^*$ *be the global optimum of* $J_n(\mathbf{x})$ *for* $\mathbf{x} \in X$.

(a) *In a competitive system (that is,* $a_{ij} \leqslant 0$ *with probability one for all* i,j*):*

(i) $J_n(\mathbf{y})$ *is concave for all* n.
(ii) *If* $\mathbf{x} \geqslant \mathbf{x}_n^*$, *then* $A_n(\mathbf{x}) = \mathbf{x}_n^*$; *if* $\mathbf{x} \leqslant \mathbf{x}_n^*$, *then* $A_n(\mathbf{x}) = \mathbf{x}$; *and*

$$0 \leqslant \frac{\partial a_n^i(\mathbf{x})}{\partial x^i} \leqslant 1 \qquad \textit{for all } i.$$

(iii) *Let* I *be the set of* i*'s such that* $x^i < x_n^{*i}$, *and* I^c *the set of* i*'s such that* $x^i \geqslant x_n^{*i}$. *Then*

$$0 \leqslant \frac{\partial a_n^i(\mathbf{x})}{\partial x^j} \leqslant 1 \qquad \textit{for} \quad i \in I, \quad j \in I \cup I^c,$$

$$-1 \leqslant \frac{\partial a_n^i(\mathbf{x})}{\partial x^j} \leqslant 0 \qquad \textit{for} \quad i \in I^c, \quad j \in I.$$

(b) *In the more general system, assume* $p_i a_{ij} + p_j a_{ji} \leqslant 0$ *with probability one for all* i,j. *Then:*

(iv) $J_n(\mathbf{y})$ *is pseudoconcave for all* n.
(v) (i)–(iii) *above are valid.*

Proof. (a): $G(\mathbf{y})$ is twice differentiable. Then

$$\frac{\partial^2 G(\mathbf{y})}{\partial y^i \partial y^j} = p_i \bar{a}_{ij} + p_j \bar{a}_{ji} \leqslant 0,$$

where $\bar{a}_{ij}$ is the expected value of a_{ij}. Thus $G(\cdot)$ is concave. $\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}]$ is concave if each $s^i[\mathbf{y},\mathbf{r},\mathbf{a}]$ is concave. Again, $s^i[\mathbf{y},\mathbf{r},\mathbf{a}]$ is twice differentiable, and

$$\frac{\partial^2 s^i[\mathbf{y},\mathbf{r},\mathbf{a}]}{\partial y^i \partial y^j} = a_{ij} \leqslant 0 \qquad \text{with probability one,}$$

so $\mathbf{S}[\cdot,\cdot,\cdot]$ is concave. From the usual arguments about a dynamic-programming problem "inheriting" concavity properties through time (see [5]), this implies $J_n(\mathbf{y})$ is concave, and $f_n(\mathbf{x})$ is concave and continuous. This proves (i). Claim (ii) is immediate from the concavity of $J_n(\cdot)$ and the definition of $\mathbf{x}_n^*$ as the global optimum, since the gradient of a concave function is diagonally antitone.

Claim (iii) is proven using the monotonicity of the derivative of a concave function. That is,

$$[\nabla J_n(\mathbf{x}') - \nabla J_n(\mathbf{x})][\mathbf{x}' - \mathbf{x}] \leqslant 0.$$

In particular, if $\mathbf{x}' = \mathbf{x}_n^*$, then

$$[-\nabla J_n(\mathbf{x})][\mathbf{x}_n^* - \mathbf{x}] \leqslant 0.$$

Claim (iii) is essentially that if $x^i \leqslant x_n^{*i}$, then an optimal solution has $a_n^i(\mathbf{x}) = x^i$, no matter what the value of the other x^j. Let $\boldsymbol{\delta}^i$ be a k-vector that has value zero except at the ith component, which has value δ^i. Suppose $\mathbf{x}^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i$ is such that for all $i \in I^c$, $\nabla^i J_n(\mathbf{x}^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i) \geqslant 0$. The theorem will be true if this point is as good as any other point that decreases one or several of the species in I. Suppose not. Then

$$\begin{aligned} 0 < {} & J_n\Big(\mathbf{x}^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\lambda}^i\Big) \\ & - J_n\Big(\mathbf{x}^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i\Big) \\ = {} & -\nabla J_n\Big(\mathbf{x}^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i - \gamma\sum_{i\in I}\boldsymbol{\lambda}^i\Big)(\boldsymbol{\lambda}) \end{aligned} \tag{8}$$

by the mean-value theorem, where $0 < \gamma < 1$, and $\boldsymbol{\lambda}$ has as its ith component λ^i. However, (8) implies

$$\begin{aligned} & -\nabla J_n\Big(\mathbf{x}^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i - \gamma\sum_{i\in I}\boldsymbol{\lambda}^i\Big) \\ & \qquad \cdot \Big[\mathbf{x}_n^* - \Big(\mathbf{x}_n^* + \sum_{i\in I^c}\boldsymbol{\delta}^i - \sum_{i\in I}\boldsymbol{\delta}^i - \gamma\sum_{i\in I}\boldsymbol{\lambda}^i\Big)\Big] \geqslant 0, \end{aligned}$$

which contradicts the concavity of $J_n(\mathbf{x})$. Therefore the inequality in (8) must be reversed. This implies

$$\begin{aligned} 0 &< \frac{\partial a_n^i(\mathbf{x})}{\partial x^j}, \qquad i \in I,\quad j \in I \cup I^c, \\ 0 &\geqslant \frac{\partial a_n^i(\mathbf{x})}{\partial x^j}, \qquad i \in I^c,\quad j \in I. \end{aligned}$$

To obtain the upper and lower bounds, let $\mathbf{z} = \mathbf{x} - \mathbf{y}$ be the decision variable. Then parallel arguments (as in [5] or [4, Theorem 3]) yield identical inequalities for the optimal amount harvested. This yields the other bounds.

The proof has assumed the existence of the partial derivatives on the relative interior of X. However, an identical argument to [5, Corollary 4.2] proves their existence.

(b): The proof of the general model would be the same as for part (a), since $p_i a_{ij} + p_j a_{ji} \leqslant 0$ with probability one assures that $G(\mathbf{y})$ is concave. However, $\boldsymbol{S}[\mathbf{y}, \mathbf{r}, \mathbf{a}]$ is not necessarily concave, so the proof breaks down. The proof therefore is to show that $\boldsymbol{S}[\mathbf{y}, \mathbf{r}, \mathbf{a}]$ is a logconcave, and that an appropriate transformation of variables transforms this problem into a problem that satisfies the concavity assumptions of part (a).

For any i, and for any fixed value of $\mathbf{r}, \mathbf{a}$,

$$\frac{\partial^2}{\partial y^{i2}} \log s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}] = -\frac{1}{y^{i2}} - \frac{a_{ii}^2}{\left(1 + r^i + \Sigma_j a_{ij} y^j\right)^2},$$

$$\frac{\partial^2}{\partial y^{j2}} \log s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}] = -\frac{a_{ij}^2}{\left(1 + r^i + \Sigma_j a_{ij} y^j\right)^2},$$

$$\frac{\partial^2}{\partial y^j \partial y^k} \log s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}] = -\frac{a_{ij} a_{ik}}{\left(1 + r^i + \Sigma_i a_{ij} y^j\right)^2}.$$

The function $\log s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}]$ is concave if for any k-vector $z \geqslant 0$ we have $z \eta z \leqslant 0$ where η is the Hessian matrix of cross partial derivatives. This is equivalent to

$$-\frac{z^{i2}}{y^{i2}} - \frac{\sum\limits_{j=1}^{k} a_{ij}^2 z^{j^2} + \sum\limits_{j=1}^{k} \sum\limits_{l>j}^{k} 2 a_{jl} a_{lj} z^j z^l}{\left(1 + r^i + \sum\limits_{j=1}^{k} a_{ij} y^j\right)^2},$$

which equals

$$-\left(\frac{z^i}{y^i}\right)^2 - \left[\frac{\sum\limits_{j=1}^{k} a_{ij} z^j}{1 + r^i + \sum\limits_{j=1}^{k} a_{ij} y^j}\right]^2 \leqslant 0.$$

In the transformed problem (7), let $\mathbf{N}_t = \ln \mathbf{x}_t$, so that $\mathbf{x}_t = \exp(\mathbf{N}_t)$. Then the transformation becomes:

$$\mathbf{N}_{t+1} = \log \mathbf{S}[\mathbf{y}_t, \mathbf{r}_t, \mathbf{a}_t]$$

which is concave, and the constraint set is

$$\exp(\mathbf{N}_{t+1}) \geqslant \mathbf{y}_{t+1} \geqslant 0,$$

which is a convex set that is increasing in $\mathbf{N}_{t+1}$. Results (i), (ii), (iii) now hold for this transformed problem, and $J_n(\mathbf{y})$ is logconcave. However, $J_n(\mathbf{y})$ logconcave implies $J_n(\mathbf{y})$ is pseudoconcave, which is the desired claim (iv). ■

In the competitive system, it is straightforward to show that if $\alpha p^i(1+\bar{r}^i) < p^i$, then it is optimal to remove this species entirely at the outset. This is not necessarily true for a species that is a prey for a more valuable species, since this species has higher future value.

The usefulness of Theorem 2 is that most of the computational work is to find $\mathbf{x}_n^*$ for each n. Particularly on a discretized version of the model, any efficient search technique can be used to find $\mathbf{x}_n^*$, which should help reduce the fabled "curse of dimensionality." A second way to increase computational efficiency is to use $\mathbf{A}_1(\mathbf{x})$, the optimal policy for $\mathbf{G}(\mathbf{y})$, as a near-optimal stationary policy. This can easily be calculated by any standard routine for concave optimization. It is conjectured that this will be a good approximation to a competitive system, since the less valuable species should lose value through time, as they have more of a chance of reducing the valuable species. Thus, this "myopic" policy should be a conservative policy.

For a predator-prey system, however, the approximation should be weaker, since prey species may increase in value through time. The "myopic" policy should tend to overharvest these species.

In either case, the effect of "optimal" harvesting should be to "simplify" the ecosystem, that is, reduce low-valued competitors, or low-valued predators that are not prey for any other species, to very low or zero levels. Even if these species are not harvested to zero, this increases the chance of their random extinction. Simplification of the ecosystem through harvesting places great reliance on the accuracy of the model, particularly to population ranges that have never been observed, but may come about due to harvesting. This suggests caution should be used in applying these results, since there exist few if any striking examples of the Lotka-Volterra equations explaining the behavior of a real ecosystem.

Silliman [9] performed laboratory studies on the competition between guppies (*Poecilia reticulata*) and red swordtail hybrids (*Xiphophorus maculatus* × *X. helleri*). The dynamics of each species can be described by a growth function which depends only on the size of that species and a linear interaction term. A discrete stochastic version of Silliman's model is

$$x_{t+1}^i = r^i(y_t^i, d_t^i) - \sum_{j \neq i} m^{ij} y^j, \qquad i,j = 1,2, \tag{9}$$
$$m^i \geqslant 0 \qquad \text{w.p. } 1,$$

where $r^i(\cdot, d^i)$ is concave, continuous, and nondecreasing for each d^i. The return from harvesting each species is assumed to be proportional to the amount harvested from that species, that is,

$$G(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{2} p^i \cdot (x^i - y^i) \qquad p^i \geq 0 \quad \text{for all } i. \tag{10}$$

Equation (9) is appropriate for two species competing for the same resource. Intuitively, one would expect that if we increase the number left of one species after harvesting, we will not decrease the number left of the second species. In fact, a stronger statement than that can be made.

The dynamic program (I) becomes

$$f_n(\mathbf{x}) = \max_{0 < \mathbf{y} < \mathbf{x}} \{J_n(\mathbf{x},\mathbf{y})\} = \sum_{i=1}^{2} p^i x^i + \max_{0 < \mathbf{y} < \mathbf{x}} \{H_n(\mathbf{y})\}, \tag{11}$$

where $H_n(\mathbf{y}) = \alpha E f_{n-1}(S[\mathbf{y}, \mathbf{d}, \mathbf{m}]) - \Sigma_{i=1}^{2} p^i y^i$ and $\mathbf{S}[\mathbf{y}, \mathbf{d}, \mathbf{m}]$ is given by Eq. (9). For all $\mathbf{x} \in X$, let $\mathbf{x}_n^0$ be the global maximum of $H_n(\mathbf{y})$. Theorem 3 states that an optimal policy for (11) "uncouples" the species in the sense that given $\mathbf{x}_n^0$, the optimal policy for each species depends only on its size relative to x_n^{0i}, regardless of the size of the competing species.

THEOREM 3

If for each n, $\mathbf{x}_n^0$ is a global optimum of $H_n(\cdot)$ given in (11), *then for each n and all $\mathbf{x} \in X$,*

$$A_n(\mathbf{x}) = \mathbf{x} \wedge \mathbf{x}_n^0,$$

where $\mathbf{a} \wedge \mathbf{b}$ denotes component-by-component minimums.

Proof. A proof similar to that of Theorem 3 in [4] shows that $H_n(\mathbf{y})$ is concave and continuous in $\mathbf{y}$ and that $f_n(\mathbf{x})$ is concave, continuous, and nondecreasing.

If $\mathbf{x} \geq \mathbf{x}_n^0$, then clearly $\mathbf{A}_n(\mathbf{x}) = \mathbf{x}_n^0$, since $\mathbf{x}_n^0$ is by definition a global optimum. Otherwise, it is necessary to show that if $\mathbf{x}^1 \geq \mathbf{x}$, then $\mathbf{A}_n(\mathbf{x}^1) \geq \mathbf{A}_n(\mathbf{x})$.

Let $\boldsymbol{\delta}^i$ be the column vector that has zero in every coordinate except the ith, which has the value $\delta \geq 0$. Suppose $\mathbf{A}_n(\mathbf{x})$ has been found for some $\mathbf{x} \in X$. Then it is clear that

$$a_n^i(\mathbf{x} + \boldsymbol{\delta}^i) \geq a_n^i(\mathbf{x}),$$

since if it were lower, the resulting value would have to be dominated by $A_n(\mathbf{x})$, which is feasible and by definition no less in value. It therefore remains to show that

$$a_n^j(\mathbf{x}+\boldsymbol{\delta}^i) \geqslant a_n^j(\mathbf{x}).$$

At $n=2$,

$$\begin{aligned} H_2(y) &= p^1\{aE[r^1(y^1,d^1) - m^{12}y^2] - y^1\} \\ &\quad + p^2\{\alpha E[r^2(y^2,d^2) - m^{21}y^1] - y^2\} \\ &= [ap^1Er^1(y^1,d^1) - p^1y^1 - \alpha p^2E(m^{21}y^1)] \\ &\quad + [\alpha p^2Er^2(y^2,d^2) - p^2y^2 - \alpha p^1E(m^{12}y^2)], \end{aligned}$$

which is the sum of two concave functions, one of which depends only on y^1 and the other only on y^2. Therefore, at $r=2$, it is true that:

(i) $\mathbf{A}_2(\mathbf{x}') \geqslant \mathbf{A}_2(\mathbf{x})$ if $\mathbf{x}' \geqslant \mathbf{x}$,
(ii) $\nabla^i H_2(\mathbf{y})$ is nonincreasing in y^i,
(iii) $\nabla^i H_2(\mathbf{y})$ is nondecreasing in y^j.

Assume as an inductive hypothesis that (i), (ii), and (iii) are valid in periods $2,3,\ldots,n-1$. Then at period n,

$$\begin{aligned} \nabla^j H_n(\mathbf{y}) &= E\{[\alpha p^i + [\nabla^i H_{n-1}(\mathbf{S}[\mathbf{y},\mathbf{d},\mathbf{m}] \wedge \mathbf{x}_{n-1}^0) - p^i]^+](-m^{ij})\} \\ &\quad + E\{[\alpha p^j + [\nabla^j H_{n-1}(\mathbf{S}[\mathbf{y},\mathbf{d},\mathbf{m}] \wedge \mathbf{x}_{n-1}^0) - p^j]^+](r^{j[1]}(y^j,d^j))\} - p^j. \end{aligned} \tag{12}$$

If y^i is increased, $s^i[\mathbf{y},\mathbf{d},\mathbf{m}]$ is not decreased, and $s^j[\mathbf{y},\mathbf{d},\mathbf{m}]$ is not increased, so by (ii) and (iii), $\nabla^i H_{n-1}$ is not increased. Since $(-m^{ij}) \leqslant 0$ with probability 1, then the first term is nondecreasing in y^i. Similarly, if y^i is increased, $s^i[\mathbf{y},\mathbf{d},\mathbf{m}]$ is not decreased, and $s^j[\mathbf{y},\mathbf{d},\mathbf{m}]$ is not increased. By (ii) and (iii), this implies $\nabla^j H_{n-1}$ is not decreased. Since by assumption $r^{j[1]}$ is nonnegative, then the second term is nondecreasing in y^i.

What has been shown is that

$$\nabla^j H_n(\mathbf{y}+\boldsymbol{\delta}^i) \geqslant \nabla^j H_n(\mathbf{y}).$$

In particular, $\nabla^j H_n(\mathbf{A}_n(\mathbf{x})+\gamma^i) \geqslant \nabla^j H_n(\mathbf{A}_n(\mathbf{x}))$ for $0 \leqslant \gamma^i \leqslant \delta^i$. By the necessary and sufficient conditions for an optimum of a constrained concave function, this implies

$$\mathbf{A}_n(\mathbf{x}+\boldsymbol{\delta}^i) \geqslant \mathbf{A}_n(\mathbf{x}). \tag{13}$$

To see that (13) together with (ii) and (iii) implies the theorem, note that for $\mathbf{x} \geqslant \mathbf{x}_n^0$ the theorem is obvious. Because of (13) and (ii) and (iii), for $\mathbf{x} < \mathbf{x}_n^0$, $\nabla^i H_n(\mathbf{x}) \geqslant 0$ for $i=1,2$; hence $\mathbf{x}$ is optimal. If $x^i > x_n^{0i}$ and $x^j < x_n^{0j}$, then from (iii), $\nabla^i H_n(\mathbf{x}\wedge\mathbf{x}_n^0) \leqslant \nabla^i H_n(\mathbf{x}_n^0)$, which implies $a_n^i(\mathbf{x}) \leqslant a_n^i(\mathbf{x}_n^0)$. Similarly, (ii) implies $\nabla^j H_n(\mathbf{x}\wedge\mathbf{x}_n^0) \geqslant \nabla^j H_n(\mathbf{x}_n^0)$, so that $a_n^j(\mathbf{x}) = x^j$. However, increasing a coordinate at a time, it is straightforward to show that if $a_n^i(\mathbf{x}) < x_n^{0^i}$, then (13) would be violated.

The induction is complete if (i), (ii), and (iii) can be shown for period n. (i) and (iii) have already been proven; (ii) follows from concavity. ■

An optimal policy from Theorem 3 is shown in Fig. 1, where $\mathbf{x}_n^0 = (x_n^{0^1}, x_n^{0^2})$. The policy has four regions, depending on whether or not x^{0^i} is obtainable from the present population size.

As n becomes large, $\mathbf{x}_n^0$ will tend to a single vector $\mathbf{x}^0$. If $p^1 \gg p^2$, it is expected that an optimal policy will reduce one of the competitors to very low levels, while maintaining the more valuable species near its single-species base stock size. This "simplification" of the population dynamics is not, in most instances, a desirable feature, particularly if we have doubts that the model contains enough "richness" to accurately portray this simplified ecosystem. Extensions to more than two species are possible given similar assumptions.

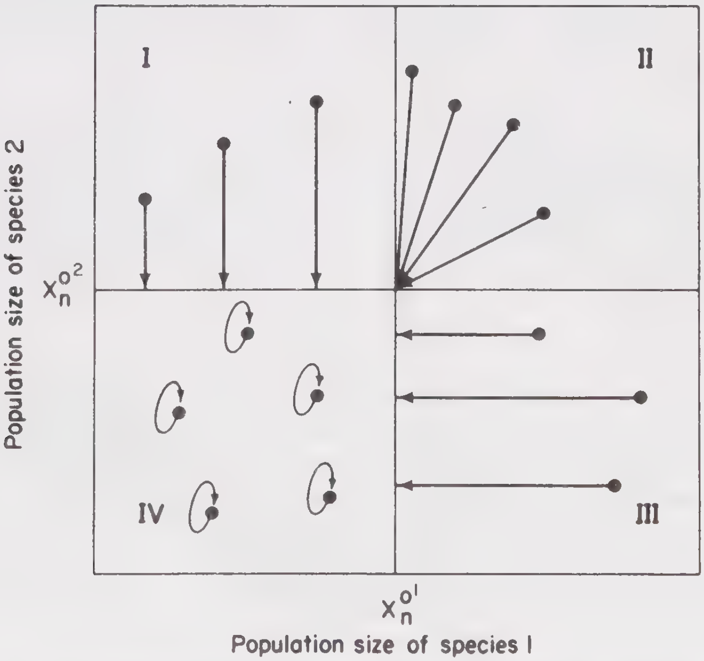

FIG. 1. Optional harvesting strategy for Silliman model at period n. In zone I, species 2 is harvested to $x_n^{0^2}$; species 1 is not harvested. In zone II, species 1 and 2 are harvested to $x_n^{0^1}, x_n^{0^2}$ respectively. In zone III, species 1 is harvested to $x_n^{0^1}$; species 2 is not harvested. In zone IV, neither species is harvested.

A simple predator-prey model analogous to the species competition model given by Eq. (9) is

$$\begin{aligned} x_{t+1}^1 &= by_t^1 + m^2 y_t^2 - r^1(y_t^1, d_t^1), \\ x_{t+1}^2 &= r^2(y^2, d^2) - m^1 y^1, \\ b, m^1, m^2 &\geqslant 0 \qquad \text{w.p. } 1. \end{aligned} \tag{14}$$

Here species 1 is the predator. It grows at a rate which is a mixture of its own population size and that of its prey, and decreases by a convex, nondecreasing function of its own population size, $r^1(y^1, d^1)$. Species 2 is the prey species. It increases by a concave function $r^2(y^2, d^2)$ and decreases by predation at a random rate $m^1 y^1$.

Let ξ be a realization of the random variable d^1, and η a realization of b. Corollary 3 assumes that $\eta - r^{1[1]}(\cdot, \xi) \leqslant 0$ for all possible combinations of (η, ξ). This is equivalent to assuming that the predator population is nonincreasing in size without the presence of the prey. This would be true of an exclusive predator, which is not usual for fish species. However, the corollary gives insight into how harvesting will affect the ecosystem. The proof of Corollary 3 is not given, since given the above assumption, it is identical to that given for Theorem 3.

COROLLARY 3

If, in Theorem 3, $\mathbf{S}[\mathbf{y}, \mathbf{d}, \mathbf{b}, \mathbf{m}]$ *is given by Eq.* (14) *instead of* (9), *with* $(\mathbf{d}, \mathbf{b}, \mathbf{m})$ *possibly random,* $r^1(\cdot, d^1)$ *convex, continuous, and nondecreasing for each* d^1, *and* $r^2(\cdot, d^2)$ *concave, continuous, and nondecreasing for each* d^2, *then for each* n *and all* $\mathbf{x} \in X$, *there exists an* $\mathbf{x}_n^0$ *such that an optimal policy is given by*

$$\mathbf{A}_n(\mathbf{x}) = \mathbf{x}_n^0 \wedge \mathbf{x}.$$

Similarly to Theorem 3, $\mathbf{x}_n^0$ should tend to some $\mathbf{x}^0$ as n gets large. If the prey species is much more valuable than the predator, an optimal policy will be to leave the predator at very low population sizes, and the prey close to a single-species optimum. If the predator is the more valuable species, then an optimal policy will tend to a prey population size that gives maximum growth to the predator. The prey should then be only a secondary or marginal component of the catch. This behavior is often observed in mixed fisheries.

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Pareto Optimal Policies for Harvesting with Multiple Objectives

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ABSTRACT

The standard recursive function formulation of dynamic programming is shown to extend readily to a problem with multiple objectives. A stochastic model is formulated which is relevant to capital accumulation models, renewable resource management, and economic growth. For relevant special cases, it is proven that the knowledge of the single objective optimal policy functions is sufficient to completely describe the set of dynamically Pareto optimal (or nondominated) policy functions for the multiple objective problem. It is also shown that there is a single policy which is optimal for three related problems: When each objective is given even weighting; when the total "regret" is minimized; and when the maximum regret is minimized.

I. INTRODUCTION

Most models of stochastic decisionmaking concentrate on optimal policies for single objectives, while most decisionmaking situations involve multiple, often conflicting objectives. While single objective optimization can be informative to the decisionmaker, it does not provide any idea of the tradeoffs involved. In this paper the usual dynamic programming formulation for stochastic models is shown to readily extend to stochastic models with multiple objectives. This fact is then used to characterize the dynamic Pareto optimal set for a class of models relevant to capital accumulation and the harvesting of renewable resources.

A related extension of dynamic programming to partially ordered sets can be found in Brown and Strauch [2]. At the time an earlier version of this paper was written, Henig [6] was extending the contraction mapping formulation of Denardo [3] to multiple objectives.

The impetus for this paper comes from the recently enacted Fishery Conservation and Management Act (FCMA), which requires fishery managers to consider biological, social, and economic factors when determining an optimal yield. Usually these factors have conflicting goals, yet a single "best" policy must be determined. A starting procedure would be to

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find some desirable subset of policies, and then consider the tradeoffs between these policies. Pareto optimal, or "efficient," policies are such a class of policies.

I have shown previously [9–11] that stochastic harvesting models are structured capital accumulation models that have structured optimal policies. Similar structure in the multiple objective problem make it possible to describe the set of efficient policies solely from knowing the single objective optimal policy functions. This "uncoupling" of a k-objective problem into k single objective problems greatly increases computational efficiency, and adds insight into the structure of the set of efficient policies.

It is also possible, for this class of harvesting models, to find several policies of interest within the set of efficient policies with little extra effort. Let the k-vector J^* be the optimum optimorum vector, and let the k-vector J be the expected return from a given policy. That is, J^{*i} is the optimal expected return in a single objective problem with objective i as the sole objective. The "p-regret function" $R_P(J)$ [14] is defined as

$$R_P(J)=\begin{cases}\left(\sum_{i=1}^{k}(J^{*i}-J^i)^p\right)^{1/p}, & p<\infty,\\ \max_i (J^{*i}-J^i), & p=\infty,\end{cases}$$

and it is desired to minimize $R_p(J)$ for a fixed value of p. Attention is given to $p=1$, or (the total group regret problem) and $p=\infty$ (the Chebyshev, or minimum maximal, regret problem). A third policy of interest maximizes the unweighted sum of the two objectives. This will be termed the "equitable policy." The stochastic models of this paper have the interesting property that a policy that is equitable also minimizes $R_1(\cdot)$ and $R_\infty(\cdot)$.

II. NOTATION AND DEVELOPMENT

A Markov process is observed for T periods, $T<\infty$. The periods are subscripted by t, $1\leqslant t\leqslant T$. Alternatively, $n=T-t+1$, the number of periods remaining till the end of the planning horizon, is used to subscript the period. At the start of each period a state $x\in X$ is observed; a decision y is chosen, which may be constrained by the state to lie in some set $Y(x)$; and the random transition to a state next period is given by

$$x_{t+1}=s[x_t, y_t, D_t],$$

where $D_1, D_2, \ldots, D_T$ are independent, identically distributed random variables distributed as the generic random variable D.

In each period, if state x is observed and decision $y\in Y(x)$ is chosen, k one-period rewards are received, given by $G_t(x, y)=(g_t^1(x, y),$

$g_t^2(x,y),\ldots,g_t^k(x,y))$. The ith reward is discounted by a factor α_i, $0 \leqslant \alpha_i \leqslant 1$.

Let $\delta_t(x)$ be a policy function in period t, that is, δ_t maps each $x \in X$ into $Y(x)$. An n-period policy π_n is a sequence of n policy functions, that is, $\pi_n = (\delta_n, \delta_{n-1}, \ldots, \delta_1)$.

A t-period history H_t is a sequence of feasible states, actions, and random variables

$$H_t = (x_1, y_1, D_1; x_2, y_2, D_2; \ldots; x_{t-1}, y_{t-1}, D_{t-1}; x_t)$$

The expected value of an n-period policy π_n, given a history H_{T-n+1}, is defined as

$$v_{\pi_n}(H_{T-n+1}) = E_{\pi_n}\left\{ \sum_{t=T-n}^{T} (\alpha^{t-1}G_t(x_t, y_t)) \middle| H_{T-n+1} \right\}, \tag{2.1}$$

where the addition of the vector return is coordinate by coordinate, and $\alpha^{t-1}G_t$ denotes coordinate by coordinate multiplication of g_t^i by α_i^{t-1}. Define the set V_T as

$$V_T = \{ v_{\pi_T}(x_1) : \pi_T \text{ is a feasible } T\text{-period policy} \}.$$

Then π_T^* is termed *efficient* or *Pareto optimal* if there does not exist some other policy π_T with $v_{\pi_T}(x_1) \in V_T$ such that [1]

$$v_{\pi_T}(x_1) \geqslant v_{\pi_T^*}(x_1). \tag{2.2}$$

Let $\Lambda_T = \{ v_{\pi_T} \in V_T : \pi_T \text{ is an efficient policy} \}$. The vmax, or vector maximization operator, is defined as

$$\text{vmax} : V_T \to \Lambda_T.$$

At times, a slightly abused use of vmax denotes finding efficient policies rather than efficient vectors. However, the usage should be clear from the context.

With these definitions, the n-period problem is

$$\begin{aligned} \text{vmax } v_{\pi_T}(x_1) = \text{vmax } E\left(\sum_{t=1}^{T} \alpha^{t-1} G_t(x_t, y_t) \right) & \\ \text{s.t.} \quad x_{t+1} = s[x_t, y_t, D_t], & \\ x_t \in X, \quad y_t \in Y(x). & \end{aligned} \tag{2.3}$$

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[1] When comparing two k-vectors, $x = (x^1, x^2, \ldots, x^k)$ and $y = (y^1, y^2, \ldots, y^k)$, $x = y$ implies $x^i = y^i$ for all i; $x \geqslant y$ implies $x^i \geqslant y^i$; $x \geqslant y$ implies $x \geqslant y$ but $x \neq y$; and $x > y$ implies $x^i > y^i$ for all i.

Let $f_n^{\text{eff}}(x)$ denote the set of n-period efficient return vectors when x is the observed state, and let $\oplus$ denote the addition of a given vector to every vector in a set of vectors. Thus $G_{n+1}(x,y)\oplus f_n^{\text{eff}}(x)$ adds the vector $G_{n+1}(x,y)$ to each vector in $f_n^{\text{eff}}(x)$. Theorem 2.1 proves that $f_n^{\text{eff}}(x)$ satisfies the standard dynamic programming recursive equations.

THEOREM 2.1

If $G_t(x,y)$ is bounded for every t, then in (2.3):

(i) *If a policy π_n^* is n-period efficient, then any k-period policy π_k such that $\pi_n^* = \{\delta_n, \delta_{n-1}, \dots, \delta_{n-k}, \pi_k\}$ is k-period efficient given the history H_{T-k+1}.*

(ii) *An n-period efficient policy depends on the past history only through the present state and expected efficient values, that is,*

$$v_\pi(H_t) = v_\pi(x_t).$$

(iii)

(a) *If there exists a nonempty set of dynamic efficient policies, then every efficient policy is a solution to the recursive equation*

$$f_0^{\text{eff}}(\cdot)\equiv 0,$$
$$f_n^{\text{eff}}(x)=\text{vmax}\{G_n(x,y)\oplus\alpha E f_{n-1}^{\text{eff}}(s[x,y,D]: x\in X, y\in Y(x)\}. \tag{2.4}$$

(b) *If there exists a sequence of point to set functions $A_1, A_2, \dots, A_T$ such that $A_i: X\to Y(x)$ and the set of resulting policies solve* (2.4), *then the sequence of functions $\{A_i(x)\}$ describe the set of dynamic Pareto optimal policies.*

The system of recursive equations imply that the set of dynamic efficient policies can be found by

(i) choosing an efficient decision in period n,
(ii) following any efficient policy from there onwards.

This is a subtle point, for in Sec. III it will be shown that for a class of problems, the weightings given to each objective by an efficient policy can vary through time.

III. APPLICATIONS

In this section, the system of recursive equations (2.4) and related systems of equations are used to describe dynamic efficient policies for two harvesting or consumption models. In the first model, a single stock of fish (or consumption good) is valued differently by two different user groups. This occurs in a fishery context when the government is the management that must set a quota on a fishing industry, but recreational fishermen or other interest groups also value the standing stock as an important resource. Such a situation arises in the management of the northern anchovy off the coast of California.

The second model is a single stock that is managed by a single agency, where harvesting or consumption each year must be allocated between different user groups. The agency must decide not only the total amount to be allocated, but also how much of the total allocation should be given to each user group. This model differs from related economic work in that the model is dynamic and stochastic.

Lemma 3.1 is due to Geoffrion [4], and is used throughout this section.

LEMMA 3.1

Let $f_1(x), f_2(x), \ldots, f_k(x)$ be concave functions that map a subset of $\mathbb{R}^n$ into R^1. Then the following two statements are equivalent:

(i) *x^* is an argument where*

$$\operatorname{vmax}(f_1(x), f_2(x), \ldots, f(k)) \qquad s.t. \quad x \in X$$

obtains a solution.

(ii) *x^* is an argument where*

$$\max \sum_{i=1}^{k} \lambda^i f_i(x)$$

$$s.t. \quad \sum_{i=1}^{k} \lambda^i = 1, \quad 0 \leqslant \lambda^i \leqslant 1 \text{ for all } i$$

obtains a solution for some $\lambda = (\lambda^1, \lambda^2, \ldots, \lambda^k)$. ■

Let x_t denote the population size at the beginning of period t, and let y_t be the population size remaining after harvesting has ceased. The transition to x_{t+1} depends only on y_t and the random variable D_t, that is,

$$x_{t+1} = s[y_t, D_t].$$

It is assumed that:

(i) $s[\cdot, d]$ is concave and continuous for each realization d of D_t. Each user group's one-period return or utility is assumed to be a function of the amount harvested, $x_t - y_t$. This is a simplifying assumption, as for some fisheries the cost of fishing varies greatly with the amount available at the beginning of the period. However, most of the results do not depend on this assumption so much as on the following two assumptions, which are assumed to be valid for $g^i(\cdot)$ for each user group i.

(ii) $g^i(\cdot)$ is concave, bounded, and continuous on the set $C=\{(x,y): x\in X, 0\leqslant y\leqslant x\}$

(iii) $g^i(\cdot)$ is nondecreasing. (For the more general case, an additional assumption that $g^{[2]}(\cdot,y)$ is nondecreasing in x is needed.)

These assumptions are discussed in more detail in [9–11].

With n periods remaining till the end of the planning horizon, and for any $x\in X$, assume that all k single objective policy functions $A_n^1(x), A_n^2(x),\ldots, A_n^k(x)$ are known, and reorder the index such that

$$A_n^1(x)\leqslant A_n^2(x)\leqslant \cdots \leqslant A_n^k(x).$$

Let $A_n(x,\lambda)$ be an optimal policy in period n for $x\in X$ and given weights λ.

THEOREM 3.1

Assumptions (i)–(iii) *imply for the problem given in* (2.4) *that for each n and every* $x\in X$:

(i) *A decision y is part of an efficient policy if and only if*

$$A_n^1(x)\leqslant y\leqslant A_n^k(x).$$

(ii) *The set of dynamic efficient policies is to choose any y as in* (i), *and then follow any* $(n-1)$*-period efficient policy thereafter.*

Theorem 3.1 decomposes the multiple objective problem into k single objective problems. Moreover, since every solution implies a relative weighting to the different objectives, part (ii) of the theorem states that there exist dynamic efficient policies whose relative weighting can shift through time. This at first seems unreasonable, but two explanations can be given to this fact. A shift of weighting can be thought of as an adjustment to the realization of the stochastic process, rather than to its expected value. The realization may overly favor one group over another, and a shift in weightings can serve as a correction.

Secondly, a shift in weightings can be viewed as a learning process. A decisionmaker's preference may in fact switch as he or she learns more about the actual consequences of their decisions.

If the largest and the smallest values of the set of efficient policies greatly differ in value, then the set of efficient policies does not lend much insight. An initial starting point for a good decision might be $y=(1/k)[\sum_{i=1}^k A_n^i(x)]$. Corollary 3.1 suggests a second policy with desirable properties.

COROLLARY 3.1

The assumptions of Theorem 3.1 *imply that for each n and every $x \in X$, an equitable policy also minimizes the total group regret and minimizes the maximum regret.*

Proof. The equitable policy by definition maximizes the total even weighted sum of the objectives. Therefore it must minimize the total deviation from the optimum optimorum vector.

Zangwill [15] proves that if k functions $g_1(x), g_2(x), \ldots, g_k(x)$ are pseudoconcave, then necessary and sufficient conditions in order to

$$\max_x \min_i \{g_i(x)\}$$

are

$$\sum_{i=1}^{k} \nabla^i g^i(x) \cdot \omega^i = 0, \qquad \omega^i \geqslant 0,$$

$$\sum_i \omega^i > 0.$$

$R_\infty(J)$ is to

$$\min_x \max_i \{J_i^* - J_i\},$$

where $J_i^* - J_i$ is convex. This is equivalent to

$$\max_x \min_i \{J_i - J_i^*\},$$

where $J_i - J_i^*$ is concave.

The above necessary and sufficient conditions, however, are identically the Kuhn-Tucker conditions for the dynamic programming problem [8] with equal weights. ■

The second model concerns the dynamic allocation of a catch quota between user groups. Let z_t^i be the amount of the catch allotted to group i in period t. Assume each user group's one-period return satisfies assumptions (i)–(iii), as well as

(iv) $g_t^i(z_t) = g_t^i(z_t^i)$, $i = 1, \ldots, k$,

that is, each user group's return depends only on the amount that it harvests, independent of the one-period harvest of the other groups.

Assume $z_n^1(x), \ldots, z_n^k(x)$, are optimal policy functions for each group when they are the only one considered, and for convenience the numbering will always be such that they are in ascending order.

THEOREM 3.2

For each n and every $x \in X$, assumptions (i)–(iv) *imply the following:*

(i) $z_n=(z_n^1,\ldots,z_n^k)$ *is part of an efficient policy if and only if* $z_n^1(x) \leqslant \sum_{i=1}^k z_n^i \leqslant z_n^k(x)$.

(ii) *For any fixed total harvest z, let z^* be the solution to*

$$\text{maximize} \quad \sum_{i=1}^{k} \lambda^i g^i(z^i)$$

$$\text{s.t.} \quad \sum_{i=1}^{k} z^i = z; \quad \sum_{i=1}^{k} \lambda^i = 1, \ 0 \leqslant \lambda^i \leqslant 1. \tag{3.2}$$

Then the dynamic recursion can be decomposed into finding an optimal $z=\sum_{i=1}^k z^i$, *and allocating the total according to* (3.2).

(iii) *A dynamic efficient policy is to choose z_n as in* (i), *and following any efficient policy till the end of the planning horizon.*

Theorem 3.2 has intuitive economic appeal. It states that while the total quota may vary according to the state observed and the period, the allocation, given a fixed quota, is the same in each period.

Theorem 3.2 also states that it is not desirable *in the long run* to have a quota smaller than that which is the smallest desired for any single user, nor larger than that desired by any user. This is true, even though some if not all users will be receiving less than their sole optimum catch as their share of the catch. Each share will be determined by the relative weights given the k objectives.

COROLLARY 3.2

The assumptions of Theorem 3.2 imply that an equitable policy also minimizes the total group regret and minimizes the maximum regret.

Proof. Same as that for Corollary 3.1. ■

IV. DISCUSSION AND EXTENSIONS

Theorem 2.1 presents a methodology for, and Theorems 3.1 and 3.2 describe efficient policies for, a class of multiple objective problems related to consumption or harvesting models. Traditionally in economics, conflicting objectives or allocations have been treated by pricing mechanisms. Unfortunately, many of the objectives in managing natural resources are difficult to price, but a utility function or preference ordering is often easy to define.

It is also clear that for any efficient policy chosen, the weights λ^i act as relative prices of the different objectives of the user groups. Each efficient policy has an imputed relative price, which can then be determined. The knowledge of the imputed relative prices may cause the decisionmaker to reconsider the decision; even if not, the methodology of this paper avoids some of the artificial pricing schemes that have been developed to evaluate natural resources.

Theorem 3.2 as stated is more appropriate for allocation among groups of users than for allocation among individual harvesters or firms. In the latter case, capacity constraints would more readily enter the model. As long as the concavity assumptions of Sec. III remain valid, and only simple upper and lower bounds are included for each firm, then the results of Theorem 3.2 can be extended readily to the level of the firm.

For many harvesting models, effort rather than catch is the decision variable. For a reasonable set of assumptions, this difference is more apparent than real. Let E be the total effort. Assume total catch is a function of total effort, i.e., $z=h(x, E)$, where $h(\cdot, E)$ is nondecreasing and continuous and $h(x, \cdot)$ is nondecreasing and continuous, and when appropriate, $z^i=(E^i/E)h(x, E)$, that is, the ith user's catch is proportional to its proportion of the total fishing effort. Finally, assume the one-period return satisfies (i)–(iii) in terms of the catch and population size, perhaps for the more general form $g^i(x, y)$.

For Theorem 3.1, note that the catch $z=h(x, E)$, so that y_t is bounded by $h(x, E_{\min})\leqslant y_t\leqslant h(x, E_{\max})$, where $y_t=x_t-h(x_t, E_t)$. The analysis then proceeds as in Theorem 3.1. For the problem of allocating the catch as in Theorem 3.2, note that $z=h(x, E)$, and $z^i=(E^i/E)h(x, E)$. A similar argument to that in Theorem 3.2 shows that the total catch is bounded by $h(x, E_{\min})\leqslant z\leqslant h(x, E_{\max})$, and that given the total catch (i.e., given the total effort) and the ith group's effort, then $z^i=(E^i/E)z$, or conversely, given the total catch and the catch of the ith user group, $E^i=E(z^i/z)$.

The above establishes a one to one correspondence between the results about the catch and the results for some models based on effort. The assumptions relating catch and effort are standard; see for example Anderson [1] or Ricker [12].

A major weakness of Theorem 3.2 is that while the user groups fish on the same stock, the total catch does not influence the return to the ith group, that is, the groups either do not supply the same market, or else have no effect on the price each receives. A more realistic assumption would be that each user group's return is of the form

$$p^i\left(\sum_{j=1}^{k} z^j\right)\cdot z^i,$$

so that the total catch affects the price received. I conjecture that as long as concavity is maintained, most of the stated results should be valid for this model.

APPENDIX

Proof of Theorem 2.1. The inductive proof follows the standard proof of stochastic dynamic programming, and hence will only be outlined. At $n=1$, the proof is straightforward.

As an inductive hypothesis, assume the theorem is true in periods $1,2,\ldots, n-1$. Then at period n, π_n^* is efficient only if there is no π_n such that

$$\omega_{T-n+1}+v_{\pi_n}(H_{T-n+1})\geqslant \omega_{T-n+1}+v_{\pi_n^*}(H_{T-n+1}),$$

where ω_{T-n+1} is the value of H_{T-n+1}. Since (ii) is valid at all periods, this implies

$$v_{\pi_n}(x_n)\geqslant v_{\pi_n^*}(x_n),$$

which proves (i).

If at period n, π_{n-1} is not efficient but $\pi_n(y,\pi_{n-1})$ is efficient, define a new policy $\pi_n^*=(y,\pi_{n-1}^*)$ where π_{n-1}^* is an efficient policy. Then π_n^* clearly dominates π_n, contradicting the assumed efficiency of π_n. Combining results yields the desired system of recursive equations. ■

Proof of Theorem 3.1. The proof is by induction on k, first showing that the theorem is valid at $k=2$, and then showing that if the theorem is valid at $k=l$, then it is valid at $k=l+1$.

$k=2$. From [4], it follows that $A_n(x,\lambda)$ is continuous in λ for fixed x, for each n and all $x\in X$. Since at $\lambda=0$ we have $A_n(x,0)=A_n^1(x)$, and at $\lambda=1$ we have $A_n(x,1)=A_n^2(x)$, continuity implies the entire interval $[A_n^1(x), A_n^2(x)]$ must be optimal for some value of λ, $0<\lambda<1$. It remains to show that no value outside the interval is optimal for some value of λ.

Assume that at $\bar{\lambda}$, $0<\bar{\lambda}<1$, we have $A_n(x,\bar{\lambda})<A_n^1(x)$. Since $A_n(x,\cdot)$ is continuous on $[0,1]$, from the definition of continuity, for any $\lambda\in[0,1]$,

$$|A_n(x,1)-A_n(x,\lambda)|<A_n^2(x)-A_n^1(x),$$

since the distance between $A_n(x,1)$ and $A_n(x,0)$ is $A_n^2(x)-A_n^1(x)$. If $A_n(x,\bar{\lambda})$ were less than $A_n^1(x)$, the inequality would be violated, contradicting the continuity of $A_n(x,\cdot)$.

A similar argument holds for $A_n(x,\lambda)>A_n^2(x)$, by using the continuity of $A_n(x,\lambda)$ at $\lambda=0$.

$k=l+1$. Suppose the theorem is valid for $k=l$. The induction is to show that for $k=l+1$, the problem can be transformed into an equivalent two-objective problem.

Let $\gamma=(\gamma^1, \gamma^2,\dots, \gamma^l)$ be such that $0\leqslant \gamma^i\leqslant 1$, $i=1,\dots, l$, $\Sigma_{i=1}^l\gamma^i=1$. Consider the weighted objective

$$\lambda\left(\sum_{i=1}^{l}\gamma^i g^i(z)\right)+(1-\lambda)g^{l+1}(z). \tag{3.1}$$

By appropriate choice of λ and γ, this weighted objective can be made to take on all values as if an $(l+1)$-vector λ were chosen with $0\leqslant\lambda^i\leqslant 1$, $\Sigma_{i=1}^{l+1}\gamma^i=1$. By the induction hypothesis, the optimum for the l objectives must lie between the largest and smallest. From above, the $k=2$ case has the same property, and the $(l+1)$-objective problem has been transformed into an equivalent two-objective problem in (3.1).

Theorem 2.1 proves part (ii). ■

Proof of Theorem 3.2. By Lemma 3.1, all efficient policies must solve, for some value of λ,

$$f_0(\cdot)\equiv 0,$$

$$f_n(x)=\max_{\Sigma_i z^i<x}\left\{\sum_{i=1}^{k}\lambda^i g^i(z^i)+\alpha Ef_{n-1}\left(s\left[x-\sum_{i=1}^{k}z^i, d\right]\right)\right\}.$$

The proof uses a transformation introduced by Karush [7] and later exploited by Veinott [13]. Let $w^1=z^1$, $w^2=z^2+z^1,\dots, w^k=\Sigma_{i=1}^k z^k$. The recursion becomes

$$f_n(x)=\max_{\substack{0<w^1<w^2\\ w^2<w^3<w^4\\ \vdots\\ w^{k-1}<w^k\leqslant x}}\left\{\sum_{i=1}^{k}\lambda^i g^i(w^i-w^{i-1})+\alpha Ef_{n-1}(s[x-w^k, d])\right\}$$

Assume $w^2, w^3,\dots, w^k$ are fixed. Then the optimum for w^1 is to

$$\underset{0<w^1<w^2}{\text{maximize}}\quad \lambda^1 g^1(w^1)+\lambda^2 g^2(w^2-w^1)=h_1(w^2).$$

Let $A_1(w^2)$ be the solution of $h_1(w^2)$ for each w^2. Then by standard dynamic programming arguments as in [11], $h_1(w^2)$ is concave, continuous, and nondecreasing in w^2. This argument can be repeated till the recursion can be written as

$$\begin{aligned} f_n(x)=\max_{0<w^k<x}\{&h_{k-1}(w^k)+\lambda^k g^k(w^k-A_{k-1}(w^k))\\ &+\alpha Ef_{n-1}(s[x-w^k, d])\}\end{aligned}$$

where $h_{k-1}(w^k)$ is concave, continuous, and nondecreasing, and $g^k(w^k - A_{k-1}(w^k))$ is concave in w^k. This proves (ii), as the problem has been transformed into one that depends only on w^k, and an allocation given w^k that solves (3.2). The proof of (i) again is by induction on k.

$k=2$. From [4], an optimal solution is continuous in λ on $[0,1]$. Since at $\lambda=0$ an optimal total amount to be harvested is $z_n^{2*}(x)$, and at $\lambda=1$ an optimal total amount to be harvested is $z_n^{1*}(x)$, then continuity implies every total harvest in the interval $[z_n^{1*}(x), z_n^{2*}(x)]$ must also be part of an efficient policy. Therefore, it remains to be proved that no total harvest outside of the interval is part of an efficient policy. However, the same continuity arguments as those in Theorem 3.1 imply this result.

$k=l$. The inductive argument is the same as that in Theorem 3.1. Theorem 2.1 proves part (iii). ■

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A Systematic Approach to Determining Mean-Variance Tradeoffs When Managing Randomly Varying Populations

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ABSTRACT

New results by Henig [3] and White and Kim [11] on multiobjective Markov decision processes are combined with an approach to smooth out year-to-year fluctuations in harvest size, to produce a systematic method for determining mean-variance tradeoffs when harvesting a random population. Further procedures for accelerating computations also are discussed, and a salmon model suggested by Mathews [4] is used to illustrate the procedure. The suggested procedure generalizes Beddington and May [1] and May et al. [5], by presenting a systematic method to determine mean-variance tradeoffs, and secondly by allowing for a much larger class of harvesting policies to be considered.

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1. INTRODUCTION

In several recent papers, Beddington and May [1] and May et al. [5] have raised the issue of high variances in the equilibrium harvests when stochastic populations are harvested at high levels. Their concerns suggest that there may be desirable tradeoffs between the average per-period harvest and the long-run (ergodic) variance of the harvests. In order to determine this tradeoff in a practical manner, what is needed is a systematic method to determine the mean-variance tradeoff among some subset of policies with desirable properties.

In this paper, such a methodology is suggested. New results by Henig [3] and White and Kim [11] on multiobjective Markov decision problems are combined with an approach to smooth out year-to-year fluctuations in the harvest size, an approach studied analytically in Mendelssohn [6]. This leads to a systematic tradeoff of the mean and variance for only a subset of policies that are Pareto optimal policies for two well-defined objectives. The algorithm is applied to a model suggested by Mathews [4] for salmon runs off Bristol Bay, Alaska. Section 2 describes the model and the objective functions to be considered. Section 3 discusses the solution procedure and

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computational considerations. Section 4 shows the results of the analysis when applied to the example.

2. THE MODEL

A population is to be managed over an infinite planning horizon. At the start of each period t, an initial population size x_t is observed. During period t an amount z_t is harvested, leaving a population size of $y_t = x_t - z_t$ at the end of the period. The population size x_{t+1} at the start of the next period is a random function of y_t and of a random variable D_t, that is,

$$x_{t+1} = s[y_t, D_t] \tag{2.1}$$

where the random variables $D_1, D_2, D_3, \ldots$ are assumed to be independent and identically distributed as the generic random variable D. If a population size x is observed and a decision y is made, an expected one-period return of $g(x, y)$ is received. The returns are discounted by a factor α, $0 \leqslant \alpha < 1$, and letting E be the expectation operator, it is desired to

$$\begin{aligned} &\text{maximize} \quad E\sum_{t=1}^{\infty} \alpha^{t-1} g(x_t, y_t) \\ &\text{s.t.} \quad (2.1);\ y_t \in Y(x_t), \end{aligned} \tag{2.2}$$

where $Y(x)$ constrains the population size y that can be left given x. For $\alpha = 1$, the summation in (2.2) will not converge. The results presented can be used in this instance by allowing α to approach 1 from below. A simple example of (2.2) is to maximize total expected discounted yield, that is,

$$\begin{aligned} &\text{maximize} \quad E\sum_{t=1}^{\infty} \alpha^{t-1}(x_t - y_t) \\ &\text{s.t.} \quad (2.1);\ 0 \leqslant y_t \leqslant x_t. \end{aligned} \tag{2.3}$$

A policy that maximizes (2.2) or (2.3) may produce harvest sizes that fluctuate sharply from period to period. *This may not be undesirable.* However, it is natural to desire to obtain a feel for what is lost if these fluctuations are smoothed out. One method [6] for smoothing out the period-to-period fluctuations in harvest size is to assess a cost for any change between z_{t-1} and z_t. Specifically, suppose for any decrease in the harvest size a cost of $\lambda \cdot (z_{t-1} - z_t)$ is assessed, and for any increase in the harvest size a cost of $\varepsilon \cdot (z_t - z_{t-1})$ is assessed. Letting $e = (\lambda - \varepsilon)/2$ and $c = (\lambda + \varepsilon)/2$, this cost can be compactly represented as $e \cdot (z_{t-1} - z_t) + c \cdot |z_t - z_{t-1}|$. In [6, 7] the approach is to combine the two objective functions. That is, the new optimization problem becomes:

$$\text{maximize}\quad E\sum_{t=1}^{\infty}\alpha^{t-1}\{g(x_t,y_t)-e[z_{t-1}-(x_t-y_t)]-c|(x_t-y_t)-z_{t-1}|\}$$
$$\text{s.t.}\quad (2.1);\ y_t\in Y(x_t);\ z_t=x_t-y_t. \tag{2.4}$$

To smooth the total fluctuations, it is natural to assume $\lambda=\varepsilon$. This implies $e=0$ and $c=\lambda=\varepsilon$, so that the one-period return for any state (x, z) is

$$g(x,y)-\lambda|x-y-z|. \tag{2.5}$$

The desired tradeoff could be approximated by varying λ, solving (2.4) for each value of λ, and then calculating the ergodic distribution of each policy found. However, there is a more systematic method to achieve the same ends. Assume each period there are two separate returns, $g(x, y)$ and $-\lambda|x-y-z|$. Then it is desired to find the set of *Pareto optimal* values and associated policies.

For any policy $\delta(x)$ defined for all x in some set of possible states X, let $v_\delta=\{v_\delta^i\}$ be the vector value of expected returns when following policy δ, that is, it is a two-dimensional vector where v_δ^i is the expected return for objective i, $i=1,2$, when following policy δ. Let V be the set of all possible return vectors. Then v_{δ^*} is Pareto optimal and δ^* is a Pareto optimal policy if there exists no other $v_\delta\in V$ such that

$$\begin{aligned} v_\delta^i &\geqslant v_{\delta^*}^i \qquad \text{for}\quad i,j=1,2,\\ v_\delta^j &> v_{\delta^*}^j \qquad \text{for some } j. \end{aligned} \tag{2.6}$$

Intuitively, (2.6) says that a policy δ^* is a Pareto optimal policy if any other policy δ that increases the expected return for one objective decreases the expected return for the other objective. Thus when determining the mean-variance tradeoff, policies are included if they lower the costs due to fluctuations as they lower the "true" value of the harvest, or vice versa, increase the "true" value of the harvest if they increase the assessed cost due to fluctuations in harvest size.

Given the set of Pareto optimal policies, the ergodic distribution for each policy is calculated. The mean and variance are then readily calculated from the ergodic distributions.

3. COMPUTATIONAL TECHNIQUES AND CONSIDERATIONS

In this section an approach to finding the set of Pareto optimal policies is described. Henig [3] has provided the theoretical foundation, and White and

Kim [11] an algorithm for efficiently calculating the Pareto optimal set. Suppose the problem has been redefined on a discrete grid. Let $p(i,j,a_i)$ be the probability of going to state j from state i when the action chosen is a_i. Here a state i refers to a particular vector pair (x,z), that is, the present population size and the harvest size last period. Let $P[\delta]$ be the transition matrix for policy δ, and let $P_{(x,z)}[\delta]$ be the row of $P[\delta]$ for state (x,z). Let $r[(x,z),\delta]$ be the two-dimensional row vector of rewards when (x,z) is the state and δ is the policy, that is, $r^i[(x,z),\delta]$ is the immediate reward for objective i when (x,z) is the state and policy δ is being followed. Let γ be a two-dimensional vector such that $0 \leqslant \gamma^i \leqslant 1$ and $\Sigma_i \gamma^i = 1$. Let f be any real-valued two-dimensional vector, and define the following operators:

$$[L_\delta f](x,z) = r[(x,z),\delta]\gamma + \alpha P_{(x,z)}[\delta]f \tag{3.1a}$$

and

$$[Uf](x,z) = \max_{\delta}[L_\delta f](x,z). \tag{3.1b}$$

Let $\bar{f}$ be the unique vector where equality is obtained in (3.1b), and let δ^* be a maximizing policy. Then Henig [3, pp. 60–61] proves that δ^* is a Pareto optimal policy if and only if it is a policy where the maximum is obtained in (3.1b) for some value of γ. Writing out (3.1) specifically in our context, a policy is Pareto optimal if and only if it achieves, for some γ, the maximum of

$$\bar{f}(x,z) = \max_{y \in Y(x)} \Big\{ \gamma g(x,y) - (1-\gamma)\lambda |x-y-z| + \alpha E\bar{f}(s[y,D], x-y) \Big\}. \tag{3.2}$$

White and Kim [11] show that by including γ in the state vector, (3.2) can be treated as a partially observed Markov decision process, and use the special structure inherent in this problem to derive an efficient version of Sondik's [10] algorithm for partially observed MDPs.

The algorithm in White and Kim [11] solves a discrete-state and -action version of (3.2) simultaneously for all values of γ in the interval [0, 1]. This readily can be seen to be the equivalent of letting λ vary in (2.5). Therefore, without loss of generality, λ can be set equal to one (as can also be seen by rescaling the return function g at the outset).

Given the set of Pareto optimal policies, which must be finite in number, the ergodic probability distribution (assuming an irreducible transition

TABLE 1

Block Form of the Transition Matrix[a]

	$(x_1,z_1)(x_2,z_1)\cdots(x_N,z_1)$	$\cdots$	$(x_1,z_i)(x_2,z_i)\cdots(x_N,z_i)$	$\cdots$	$(x_1,z_N)(x_2,z_N)\cdots(x_N,z_N)$
States that have z_1 as optimal harvest (x,z)	$P_{(x,z)}(\delta^*)$		0		0
$\vdots$	$\vdots$		$\vdots$		$\vdots$
States that have z_i as optimal harvest (x,z)	0		$P_{(x,z)}(\delta^*)$		0
$\vdots$	$\vdots$		$\vdots$		$\vdots$
States that have z_N as optimal harvest (x,z)	0		0		$P_{(x,z)}(\delta^*)$

[a] $P_{(x,z)}(\delta^*)$ are the appropriate rows of $P(\delta^*)$ for an optimal policy δ^*.

matrix) can be calculated readily. Let π_0 be an initial guess at this distribution, and calculate successively for a given δ^*

$$\pi_n = \pi_{n-1}^T P[\delta^*], \tag{3.3}$$

where T denotes the vector transpose. The iterations stop when the maximum difference between π_n and π_{n-1} is at a satisfactory level.

While the iterations described in (3.3) are straightforward, they are inefficient and impractical. Suppose the population size is defined on a 25-point grid. Then there are 25 possible harvest sizes, so that there are 625 states. This implies for any policy δ^* that $P[\delta^*]$ has 390,625 entries, which would require roughly 1,562 K of computer storage. However, $P[\delta^*]$ is sparse, since if $x-\delta^*(x,z)=z'$, then a transition only can be made to states (x,z') in the next period. Permute row and columns of $P[\delta^*]$ so that the columns run through all values of x for each fixed value of z, and order the rows so that all states that harvest the same amount when following δ^* are together. This yields a blocked matrix as in Table 1. A solution procedure is to iteratively solve (3.3) for each block in order until convergence is reached. This is precisely block Jacobi iterates as described in Young [12]. The advantage is both a reduction in computer storage (since only the smaller blocks are used one at a time) and an acceleration of convergence [12, Chapter 14].

4. EXAMPLE

Mathews [4] has suggested the following model for salmon runs on the Wood River off Bristol Bay, Alaska. Let x_t be the number of recruits at the start of period t, and y_t the number of spawners at the end of period t. Then

$$x_{t+1} = \exp\{D_t\}\, 4.077 y_t \exp\{-0.800 y_t\},$$
$$D \sim \text{Normal}(0, 0.2098). \tag{4.1}$$

The example problem is defined on a grid of 15 equally spaced points on $(0,5]$ in units of 10^6 fish. The procedure used is described in detail in [7] . The constraint set $Y(x)$ is assumed to be $Y(x)=\{y: 0 \leqslant y \leqslant x\}$, α is arbitrarily set at 0.97, and the primary one-period return is simply the yield, $x_t - y_t$, while the second objective is $-\lambda|x_t - y_t - z_{t-1}|$ with $\lambda = 1$. In applications, it will be necessary to vary α to test the sensitivity of the results to the change in the discount factor.

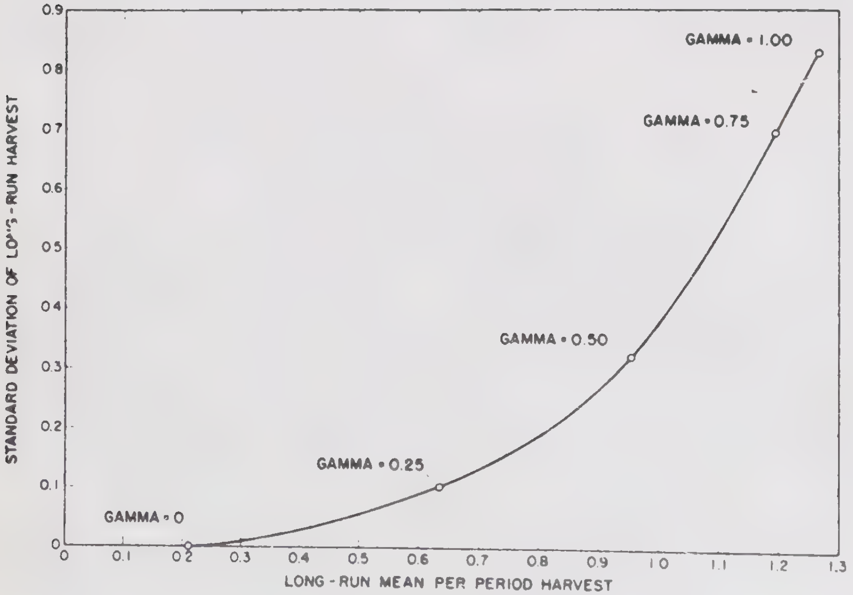

FIG. 1. Long-run (ergodic) mean–standard-deviation tradeoff for the salmon model.

The mean–standard-deviation tradeoff curve using the techniques of Sec. 3 is shown in Fig. 1. The points where $\gamma = 0.0, 0.25, 0.5, 0.75, 1.0$ are identified in order to show how the tradeoff varies with γ. It is clear from Fig. 1 that substantial reductions can be made in the standard deviation with only minimal reductions in the mean per-period harvest. At $\gamma = 0.75$ as compared with $\gamma = 1$, the mean per-period harvest has only been reduced from 1.26×10^6 to 1.2×10^6 fish (a reduction of 4.76%), while the standard deviation has been reduced from 0.83×10^6 to 0.70×10^6 fish, a reduction of 15.66%.

Figure 2 shows the change in the ergodic distribution for selected values of γ. As γ decreases, the tails become shorter, the mode higher and lower. The distribution is bimodal in the approximate range 0.8–0.6, and becomes extremely steep and narrow as γ nears zero.

Figure 3(a)–(e) shows an optimal policy for these same values of γ. The figures are read by finding the appropriate (x, z) point on the figure, following the arrow in that region; the resulting z value is an optimal harvest for that state. In region I the harvest size decreases, in region II the harvest size remains the same, and in region III the harvest size increases. Figures 2 and 3 show that as γ varies from 1.0 to 0.0, region II increases at the expense of region III, until region III disappears entirely, and while region I does not change in size, the probability of ever being in that region decreases to zero.

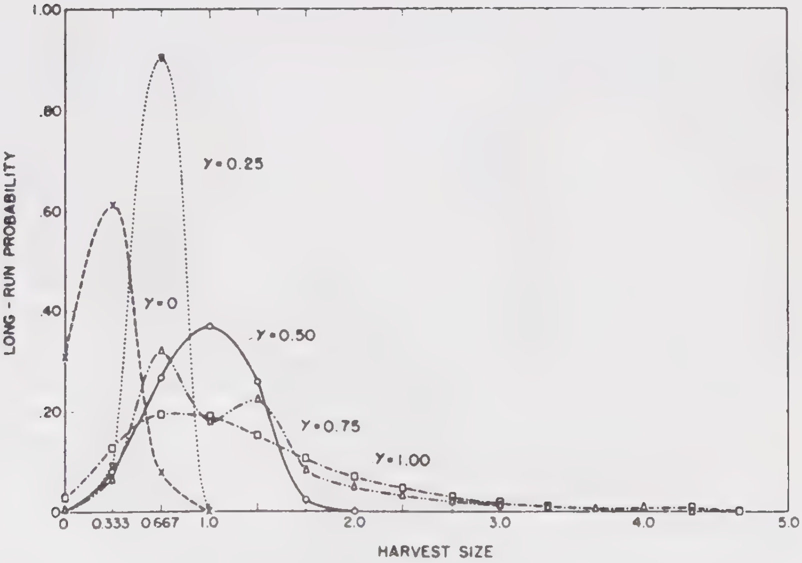

FIG. 2. Long-run (ergodic) distribution for the salmon model as γ varies.

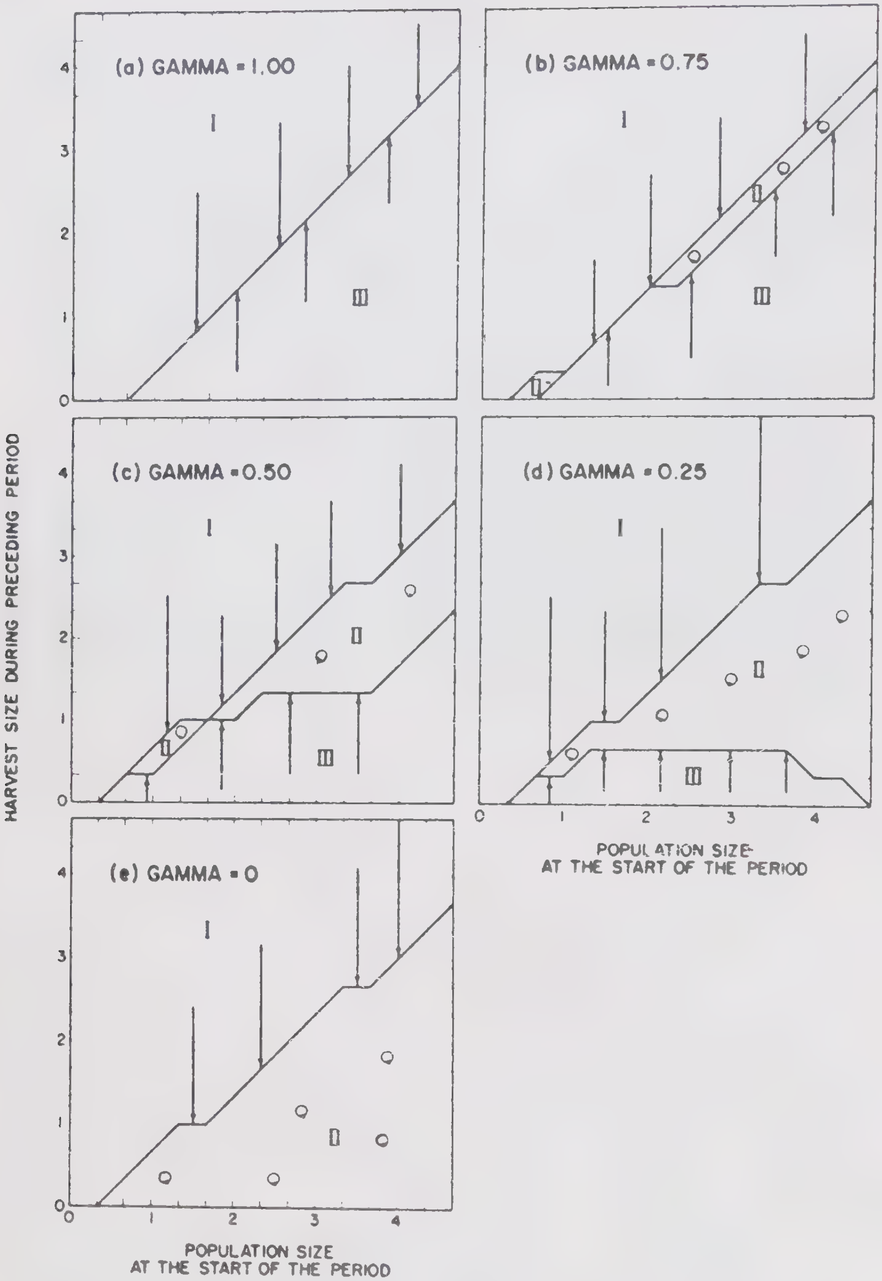

FIG. 3. Optimal policy functions for the salmon model for γ fixed at five levels.

5. DISCUSSION AND SUMMARY

New results on multiobjective Markov decision problems have been combined with an approach to smoothing harvests to produce a technique for determining the mean-variance tradeoff among the "best" subset of harvesting policies. The technique has been found to be computationally reasonable, and produces the maximum amount of information for the decisionmaker.

The suggested technique greatly extends the analysis in Beddington and May [1] and May et al. [5]. While the particular example used to illustrate the algorithm has Gaussian noise, the general formulation is not restricted to this class of models as in the cited references. Moreover, in these references, they set the growth term equal to zero, and assume that the one-period distribution of returns from any policy is equivalent to the long-run distribution of returns when following the same policy (i.e., they examine behavior when $dx/dt=0$). This assumption is very often false. The proposed optimization methods calculate explicitly the long-run distribution that arises when following a given policy. Also, by restricting the decision set $Y(x)$, the proposed models include as a subset models that require fixed effort or fixed harvests. However, since $Y(x)$ need not be so restricted, the class of decision processes that can be considered is much richer.

Moreover, fixed-effort or fixed-harvest policies arise from conclusions based on deterministic models of population dynamics, conclusions that may not be appropriate for randomly varying populations. (In practice, most fisheries management, for example, varies the estimate of maximum sustained yield each year as the population changes.) By not being restricted to fixed-effort or fixed-harvest policies, it is possible to determine what the loss in value is from using such policies. The example in Sec. 4 suggests that the best fixed-harvest policy significantly reduces the average per-period harvest. It is proven analytically in [2, 8, 9] that *optimal* harvesting policies for randomly varying populations will rarely be of the fixed-effort or fixed-harvest type.

The determination of the mean-variance tradeoff is only as good as the model that is used in the analysis. However, by providing an easy-to-understand tradeoff curve as well as much ancillary information about other characteristics of the policies under consideration, the decisionmaker is left in the best position to integrate this knowledge with other information available, both subjective and objective in nature.

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USING MARKOV DECISION MODELS AND RELATED TECHNIQUES FOR PURPOSES OTHER THAN SIMPLE OPTIMIZATION: ANALYZING THE CONSEQUENCES OF POLICY ALTERNATIVES ON THE MANAGEMENT OF SALMON RUNS

ROY MENDELSSOHN[1]

ABSTRACT

The mathematics of Markov decision processes and related techniques are used to analyze a model relevant to salmon management. It is shown that the choice of grid can have a significant effect on the results obtained. Optimal policies that maximize total expected discounted return may be too variable. Smoothing costs are included to trade off long-run total return against the smoothness of the year-to-year fluctuations in the allowed harvest. Simpler, approximate policies that have a smoothing effect are also found. Preliminary analysis suggests the results are robust against misspecification of the parameters of the model. Concepts such as maximum sustainable yield would seem to impute a very high smoothing cost and are probably not practical for fish populations with a significant degree of randomness.

The history of most managed natural populations is one of sizable, nondeterministic variations in the dynamics of the population. This observed variation tends to have two sources: The first source is actual randomness in the system, such as that due to environmental variability, which will exist no matter how accurate our models become; and the second source is the inaccurate or incomplete specification of the transition probabilities themselves. Standard production models (Schaefer 1954; Pella and Tomlinson 1969; Fox 1970, 1971, 1975) assume deterministic dynamics, as do most recent bioeconomic analyses, as in Clark (1976) or Anderson (1977). For randomly varying populations, at best only extremely low harvests may be sustainable year to year, and it is not difficult to develop realistic scenarios where policies that are sustainable in a deterministic model would cause possible depletion in a stochastic model.

In this paper, the latest tools from stochastic optimization, particularly in the area of Markov decision problems (MDP's) are used to analyze a model relevant to salmon management. The viewpoint taken is that of the analyst, who must analyze trade offs and provide a decision maker with as few policies as possible that contain the maximum amount of information, rather than that of the decision maker, who ultimately decides if a particular concern or trade off is worthwhile. The salmon model is used as an example—the goal is to gain insight into managing randomly varying populations.

Ricker (1958) appears to be the first to examine the effects of variability on management. He used intuition and simulation to arrive at policies that are of the same general form as many of the policies to be discussed in this paper. However, Ricker presented no systematic way of developing optimal policies and made the incorrect assumption that the long-run stochastic behavior will have a mean equal to the deterministic equilibrium yield, with noise around this mean.

Reed (1974) derived qualitative properties of optimal policies if the random variable has a mean of 1, if it affects the population dynamics in a multiplicative manner, and if it has costs when the system is shut down (no harvesting) and then started up again (resumption of harvesting). Reed's results are not relevant to the model discussed in this paper, since he assumed the deterministic population model is concave, while the models examined in what follows are pseudoconcave. A more complete treatment of one dimensional stochastic growth models can be found in Mendelssohn and Sobel (in press).

Walters (1975) and Walters and Hilborn (1976, 1978) discussed a variety of topics as the concerns

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of this paper. Some of the techniques they discussed, particularly the filtering techniques (Walters and Hilborn 1978), are only appropriate if the model has an additive error term. While a Ricker spawner-recruit curve can be transformed to an additive model, many models do not have this feature.

I am presenting what I feel is an improved way to smooth out the fluctuations in the year-to-year harvests as compared with the method suggested in Walters (1975) and show that the Bayesian (adaptive) model discussed in Walters and Hilborn (1976) has an optimal policy with a very simple form that can be readily calculated.

Moreover, a rigorous approach is taken to define the model on a grid and the effects of the grid choice. None of the papers cited deal with this important question; new results are presented which show that the most serious effect of the grid is on the estimates of the long-run (ergodic) probabilities of the population dynamics when following a given policy. Particularly the tail properties of the ergodic distribution, i.e., the long-run probability of low harvest or low population sizes, are misestimated. This is a new finding even in the MDP literature, and has numerical implications, particularly when calculating the trade off between the mean harvest of a given policy and the long-run probability of undesirable events when following that policy.

THE MODEL

The models to be analyzed were developed by Mathews (1967) to describe the spawner-recruit relationships of sockeye salmon, *Oncorhynchus nerka*, populations in two rivers that run into Bristol Bay, Alaska. Oceanographic and other factors affect the number of recruits to a degree where the relationships can be modeled by the random equations:

Wood River:

$$x_{t+1} = \exp(d)\,(4.077y_t)\,\exp(-0.800y_t)$$
$$d \approx N(0, 0.2098) \qquad (1.1a)$$

Branch River:

$$x_{t+1} = \exp(d)\,(4.554y_t)\,\exp(-1.845y_t)$$
$$d \approx N(0, 0.3352) \qquad (1.1b)$$

where y_t is the number of spawners in period t, x_{t+1} is the (random) number of recruits in period $t+1$, and $d \approx N(a, b)$ denotes that d is a normally distributed random variable, with mean a and variance b

For deterministic versions of Equation (1.1), the primary objective of management is MSY (maximum sustainable yield), which is equivalent to the largest per period growth of the deterministic model. The stochastic equivalent of this criterion is to maximize the average per period harvest, or gain optimality. Mathematically, letting E be the expectation operator, this is

$$\max \lim_{T \to \infty} \left[\frac{1}{T} E \sum_{t=1}^{T} (x_t - y_t) \right] . \qquad (1.2a)$$

However, for many decision making situations, total expected discounted harvest may be a preferable criterion, since a discount factor can represent a measure of risk or uncertainty about the system, over and above the variability due to the random variable d. More formally, if α is a discount factor $0 \leq \alpha < 1$, the problem is to:

$$\text{maximize } E \left[\sum_{t=1}^{\infty} \alpha^{t-1} p(x_t - y_t) \right] \qquad (1.2b)$$

subject to $0 \leq y_t \leq x_t$; and Equation (1.1)

where p is a weighting factor, which could be 1 or could represent the average weight of the salmon harvested.

All the results in this paper are for expected discounted return with $\alpha = 0.97$. For $\alpha = 1$, Equation (1.2a) must be used, since Equation (1.2b) is infinite for most policies. The choice of $\alpha = 0.97$ is arbitrary, though numerical runs for α ranging from 0.95 to 1.00 produced no significant changes in the results. When actually implementing a model, a careful choice of α must be made, and the sensitivity of the results to changes in the value of α should be tested. It should be mentioned that $\alpha = 1$ is just as much a discount factor as any other value and implies certain temporal preferences and attitudes towards risk that may not adequately reflect the decision maker's preferences.

The shortcomings of Equation (1.1a) or (1.1b) should also be noted, such as no account is taken of ocean harvesting of the salmon, particularly by a foreign nation. This just reinforces the idea that the purpose of this analysis is not optimization per se, but rather to provide the decision maker with added insight and reasonable first choices.

Defining the Model on a Discrete Grid

In order to make Equation (1.2) amenable to numerical methods, it is necessary to define both the state space and the action space on a discrete grid, and then to redefine the transition probabilities, etc., on this grid. Several authors (Fox 1973; Bertsekas 1976; Hinderer 1978; Waldmann 1978; Whitt 1978; Larraneta[2]) have suggested techniques to reduce MDP's to a grid and give bounds on the error due to the approximation. I have shown elsewhere (Mendelssohn[3]) that grid choice can have a significant effect on the analysis. An optimal policy and the value of an optimal policy may not be greatly affected by the choice of grid, but the estimated probabilistic behavior of the population dynamics is affected significantly by the choice of grid.

A first effort then is to find an adequate grid for the problem, a grid fine enough for both the desired accuracy and for realistic approximations of observed population sizes and coarse enough for computational efficiency. Increased computational efficiency makes it reasonable to solve many variations of a given model, which allows for a more thorough exploration of the management questions of interest and their sensitivity to key assumptions.

Several different grids were tried for Equation (1.2) for both the Branch and Wood Rivers.

To define Equation (1.2) on a given grid, suppose a grid of *k* points has been chosen on which to discretize the problem and assume, as is reasonable for this problem, that the reduced action space (how many spawners to leave) is equivalent to the state space (how many recruits are observed at the beginning of the period). From Equation (1.1), letting R_1 and R_2 represent the parameters of the Ricker equation

$$\begin{aligned} P(x_{t+1} \leqslant \omega | y_t) &= P[(e^d) R_1 y_t \exp(-R_2 y_t) \leqslant \omega] \\ &= P(d \leqslant \ln\omega - \ln a) \qquad (2.1) \end{aligned}$$

where $a = [R_1 y_t \exp(-R_2 y_t)]$. Let Φ be the standard normal integral for a random variable $\bar{d} = d/\sigma$, and let x_i, x_{i+1} be any two adjacent points on the grid. Then:

$$P(d \leqslant \ln x_i - \ln a) = \Phi\left(\frac{\ln x_i - \ln a}{\sigma}\right)$$

$$P(d \leqslant \ln x_{i+1} - \ln a) = \Phi\left(\frac{\ln x_{i+1} - \ln a}{\sigma}\right)$$

so that one method of defining the transition probabilities on a grid is:

$$P(x_{t+1} = x_{i+1} \mid y_t) = \Phi\left(\frac{\ln x_{i+1} - \ln a}{\sigma}\right) - \Phi\left(\frac{\ln x_i - \ln a}{\sigma}\right).$$

The discrete probability when the action is y_t is equal to the total probability of going to any state in the interval (x_i, x_{i+1}).

If zero is included as a state, the procedure needs to be modified slightly. Suppose the probability of going to x_1 is known for each decision y. Then an arbitrary fraction of this probability is assigned as going to the zero state. In this paper, one-half of the probability in the interval $(0, x_1)$ is assigned to the zero state. The results have been found not to be sensitive to the value of the fraction; this is because zero is an absorbing state. Either there exists a policy that never reaches $(0, x_1)$ and hence never reaches zero, or else with probability one the population goes to zero in finite time. Hence, it is the size of $(0, x_1)$ that most influences the results, not the fraction of this total that is assigned to going to the absorbing state.

Adding an absorbing state is sensible if the absorbing state is thought of as all states at low enough population levels such that it would take years for the fishery to recover again, if it recovers at all. Without the absorbing state, the models in Equation (1.1a, b) will always recover in fairly short order. Since fisheries can be depleted, the inclusion of an absorbing state would seem to be a more realistic assumption. It is included in what follows.

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[2] Larraneta, J. C. 1978. Approaches to approximate Markov decision processes. Paper presented at Joint National ORSA/TIMS Meeting, Nov. 13-15, 1978, Los Ang., Calif.

[3] Mendelssohn, R. 1978. The effects of grid size and approximation techniques on the solutions of Markov decision problems. SWFC Admin. Rep. 20H, 15 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv. NOAA, Honolulu, HI 96812.

A coarser grid implies, in a sense, less information about the state of the system. As the interval $(0, x_1)$ becomes large, our information has decreased about the true state of the population and this increased uncertainty is reflected in increased risk of absorbtion. Similarly, a finer grid implies more exact information—a grid should not be used which is finer than the precision of the estimate of the population size.

Optimal policies for grids of 16, 26, 51, 101, and 501 equally spaced points (including zero) for both rivers are shown in Table 1. The optimal equilibrium population for the equivalent deterministic models are shown also. All numbers are in units of millions of fish.

The optimal policies are all of the base stock variety, i.e. it is optimal to harvest to a fixed number of spawners, or else not to harvest at all. If the 501-point grid is taken as the standard, it can be seen that each coarser grid has as its base stock size the grid point closest to the base stock size for the 501-point grid.

Figure 1 gives the long-run (ergodic) cumulative distribution of being in any state when following an optimal policy on grids of 16, 26, 51, and 101 points. Grid size can be seen to play a crucial part in estimating the probabilistic behavior of the population. For the Wood River, extinction with probability one is predicted on grids of 16 and 26 points, while the probability is zero on grids of 51 and 101 points, so long as zero is not the initial state. Similar but not identical results are valid for the Branch River. It should be emphasized that for $\alpha = 1$, i.e., when the objective is given by Equation (1.2a), the estimated average per period harvest of any policy depends entirely on the ergodic distribution that arises from that policy. Therefore, this variation in estimated long-run behavior due to changes in grid size is nontrivial.

Probability one of extinction occurs because for a finite state, irreducible Markov chain with an absorbing state, the absorbing state is reached in finite time with probability one. However, for the larger grids, there exist policies that are reducible, in the sense that if the chain does not start in the interval $(0, x_1)$, it will never enter that interval. Since $P[x_t \epsilon (0, x_1)] = 0$, and a fraction of this probability has been assigned to the zero state, then $P(x_t = 0) = 0$. When using the smaller grids that induce Markov chains that are irreducible, the estimated time till absorption varies greatly also. For example, for the Branch River, if $P(x_1 = 0) = 0$ and $P(x_1 = \omega) = 1/(N-1)$, where ω is a grid point and N is the number of states, then a 16-point grid predicts absorption with probability one after 2,000 iterations, the 26-point grid predicts only a 76% chance of absorbtion after 2,000 iterations, and the 51-point grid predicts only a 17% chance of absorption.

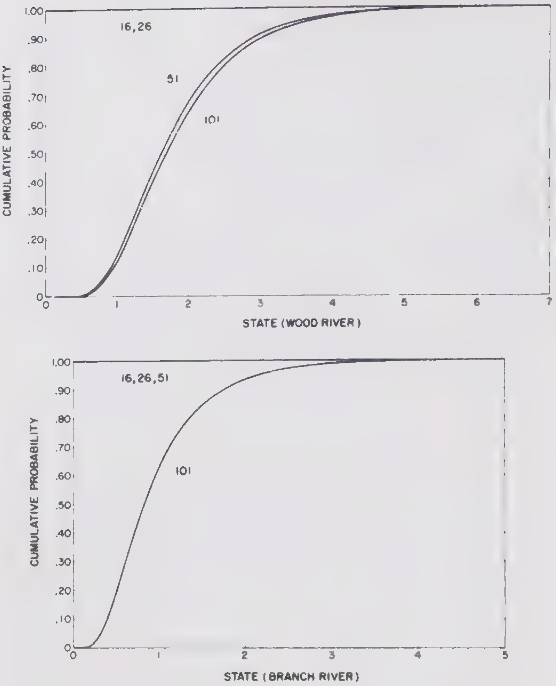

FIGURE 1.—Ergodic cumulative distributions for optimal harvesting strategies on grid sizes of 16, 26, 51, and 101 points for the Wood River and the Branch River.

TABLE 1.—Optimal policies for the different grid sizes.

Wood River	Grid size	Branch River
$y_t = \min(x_t, 0.9333)$	16	$y_t = \min(x_t, 0.3333)$
$y_t = \min(x_t, 0.840)$	26	$y_t = \min(x_t, 0.4000)$
$y_t = \min(x_t, 0.700)$	51	$y_t = \min(x_t, 0.3000)$
$y_t = \min(x_t, 0.770)$	101	$y_t = \min(x_t, 0.3500)$
$y_t = \min(x_t, 0.742)$	501	$y_t = \min(x_t, 0.3500)$
Equilibrium stock 0.735	Deterministic	Equilibrium stock 0.345

When maximizing total expected discounted return, the discounted mean return depends on the values of these intermediate probability distributions, so that coarser grids can be expected to underestimate the long-run value of the harvest.

Finally, for the Wood River, note that the 51- and 101-point grids have similar long-run behavior. These results suggest that in order to find good policies, it is only necessary to use a grid size of 26 to 51 points for the problems under consideration. However, to analyze the long-run (probabilistic) behavior of a given policy, it is necessary to use a grid containing no fewer than 100 points.

It should be reemphasized that the reason for considering a coarser grid is that a smaller problem size allows for many problems to be solved at a small cost. This is desirable to obtain insight into the sensitivity of the problem. However, it is possible to solve quite large problems, making use of a variety of methods to accelerate computations (see for example Porteus 1971; Hastings and van Nunen 1977). For example, the 501-point grid for the Branch River used 1.80 s of CPU (central processing unit) time to perform the optimization. Computations, when smoothing costs are included (see Policy Analysis section), have 2,601 states. These used about 5 to 6 min of CPU time to perform the computations, but at a cost of about $20. Our experience is that it is possible to obtain reasonable estimates using coarse grids and that this suffices for initial policy investigation. However, it is worthwhile to reanalyze the final two or three problems of greatest interest on a finer grid.

POLICY ANALYSIS

For the Wood River, the optimal policy for Equation (1.2) is given by

$$y_t = \text{minimum}\ (0.770, x_t)$$

and it produces a mean per period harvest of 1.14758, and a standard deviation in the harvest of 0.8963. The median harvest is 0.91, and no harvest occurs roughly 4.3% of the time. A harvest of 25% or less of the mean harvest occurs roughly 15% of the time, while a harvest greater than the mean harvest occurs approximately 38% of the time.

Similarly, for the Branch River, an optimal policy for Equation (1.2) is given by

$$y_t = \text{minimum}\ (0.300, x_t)$$

and it produces a mean per period harvest of 0.6622, and a standard deviation in the harvest of 0.6120. The median harvest is roughly 0.500; there is a 3.9% chance of no harvest. A harvest of 25% of the mean harvest or less occurs roughly 14.5% of the time, and a harvest greater than the mean harvest occurs approximately 61% of the time.

While these policies are similar in form to policies that are optimal for a deterministic version of Equation (1.2), they differ greatly in the year-to-year dynamics. There are two ways of finding the optimal deterministic policy. The first way is to assume a general model of the form:

$$x_{t+1} = R_1 y_t \exp(-R_2 y_t)$$

The second method is to assume a general model of the form:

$$x_{t+1} = E \exp(d) R_1 y_t \exp(-R_2 y_t)$$

where as before, R_1 and R_2 are the parameters of the Ricker equation. The second method is preferable since it uses all the information available. As d is a normal random variable with mean zero and variance σ^2, it is easy to show that $\exp(d)$ is a lognormal random variable with expectation $\exp(\frac{1}{2}\sigma^2)$. Solving for the optimum sustained yield (OSY) population size for each river gives:

	Wood River	*Branch River*
x_{OSY}	0.735	0.345
OSY	1.11346	0.63804

Both OSY values are lower than the mean per period harvests in the stochastic models, but the variation is too high to allow this amount to be harvested each year. However, the x_{OSY} level is a good estimate of the base stock size, and it is known a priori from Mendelssohn and Sobel (in press) that a base stock policy is optimal.

In the deterministic model, once x_{OSY} is reached, both the population size and the harvest size are maintained at steady, equilibrium levels. An optimal policy for the stochastic model, however, produces large fluctuations in both and may allow no harvesting 1 yr out of 25 in the long run. For many fisheries, these "boom and bust" conditions may not be acceptable. Many people, especially those with interest or mortgage payments, as are many fishermen, are concerned about smoothness of income received as well as the total amount received. The final decision on the acceptable amount of fluctuation is, of course, up to the decision maker with appropriate input.

There are several methods available to try to find a balance between the smoothness of the random income stream and its total discounted expected value. Walters (1975) and Walters and Hilborn (1978) suggested fixing a given mean harvest

u, and then finding a policy that minimizes $\lim_{T \to \infty} E \frac{1}{T} \sum_{t=1}^{T} (z_t - u)^2$. This methodology depends on the values of u chosen. It also determines the policy that minimizes the approximate long-run variance for a given long-run mean harvest. This is not equivalent to reducing the size of the year-to-year fluctuations.

A second method is to include "smoothing costs" into the one-period return. This approach has been studied analytically by Mendelssohn.[4] Let γ be the cost of a unit decrease in the harvest from year to year, and let ϵ be the cost of a unit increase in the harvest from year to year.

If z was harvested last year, then net revenues this year, for any harvest z_t, are decreased by

$$\begin{cases} \gamma(z - z_t) & \text{if } z > z_t \\ 0 & z = z_t \;. \\ \epsilon(z_t - z) & z < z_t \end{cases}$$

Amended to Equation (1.2), this would imply a one-period net benefit of

$$p(x_t - y_t) - \gamma[z - (x_t - y_t)]^+ - \epsilon[(x_t - y_t) - z]^+$$

where $(a)^+$ denotes the positive part of a. An alternate form is to let $e = (\gamma - \epsilon)/2$ and $c = (\gamma + \epsilon)/2$. Then the one-period return is:

$$p(x_t - y_t) + e(x_t - y_t) - c \,|\, (x_t - y_t) - z \,|\, - ez.$$

One advantage to the smoothing cost approach over other approaches is that p, e, and c can be normalized so as to be interpreted as relative prices. That is, the normalized values $p = 1$, e/p, and c/p can be interpreted as the value of having the between period harvest "smoothed" by one unit relative to the value of one unit of additional harvest. Actual relative values are often difficult to determine. But by parameterizing on e and c, it is possible to present a decision maker not only a range of possible "optimal" policies and their consequences, but also some feeling for the relative trade off between total income and the smoothness of the received income stream.

For the Wood and Branch Rivers, two sets of computations were performed. The first set assumes that $\gamma = \epsilon$, i.e., there is an equal concern for increases in allowable harvest as well as for decreases. This is equivalent to $e = 0.0$ and $c = \gamma$ (or equivalently ϵ). The motivation for this cost structure is that fishermen typically resist any decrease in the allowed harvest, hence $\gamma > 0$. However, allowing increases in the harvest size often signals fishermen to gear up and invest in equipment, thereby making it even more difficult to decrease the allowable harvest later on. Therefore this cost should be equal to a cost due to a decrease in the harvest.

As a counterbalance to this, a second set of computations were performed with $\gamma > 0$ but $\epsilon = 0$, i.e., a cost only if the harvest is decreased. This is equivalent to $c = e = \gamma/2$.

For the first set of computations, with $e = 0.0$ and $p = 1.0$, values of c of 0.25, 0.50, 0.75, 1.00, 1.25, 1.50, 1.75, and 2.00 were used. These are equivalent to relative values of ⅛, ¼, ⅜, ½, ⅝, ¾, ⅞, and 1. For the second set of runs, with $c = e$, and $p = 1.0$, values of 0.25, 0.50, 0.75, 1.00 and 1.25 were used. These are equivalent to a ratio of γ/p equal to ¼, ½, ¾, 1, 1¼. The results are summarized in Figure 2(a)-(m) and Figure 3(a)-(m), which show an optimal policy for each river for each of these cases. All computations were performed on 26-point grids.

The figures are read as follows. Suppose z was harvested last year and x is the observed population size this period. Find the point (x, z) on the graph and follow the arrow in that zone to the appropriate boundary as indicated. Then read off the z value of this point; this is the optimal amount to harvest during this period.

For example, if $c = 0.50$, $e = 0.00$, $x_t = 0.84$, and the harvest last period was 0.28, Figure 2(b) shows that the optimal policy for the Wood River is to harvest 0.28 this period. Note that the dashed line is the equivalent base stock harvest with no smoothing costs.

While the policies in Figures 2 and 3 are optimal for the given relative values of p, e, and c, they are complex in nature and would be difficult for a layperson to understand. Practical management often implies determining simpler, good but suboptimal policies that achieve the same objectives. These policies are often more desirable since they are easier to implement and easier to explain the rationale to the public.

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[4] Mendelssohn, R. 1976. Harvesting with smoothing costs. SWFC Admin. Rep. 9H, 26 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

As an example of suboptimal, approximate policies, the following nine modified base stock policies were examined:

Wood River

1) Base stock policy, base stock size = 0.84.
2) Policy of base stock size of 0.56 till 2.52, then a base stock size of 0.84.
3) Policy of base stock size of 0.56 till 1.40, then a base stock size of 0.84.
4) Harvest 0 till 0.28, harvest 0.28 till 0.84, a base stock size of 0.56 till 2.52, then a base stock size of 0.84.

Branch River

5) Base stock policy, base stock size of 0.40.
6) Base stock size of 0.4 till 1.6, then a base stock size of 0.6.

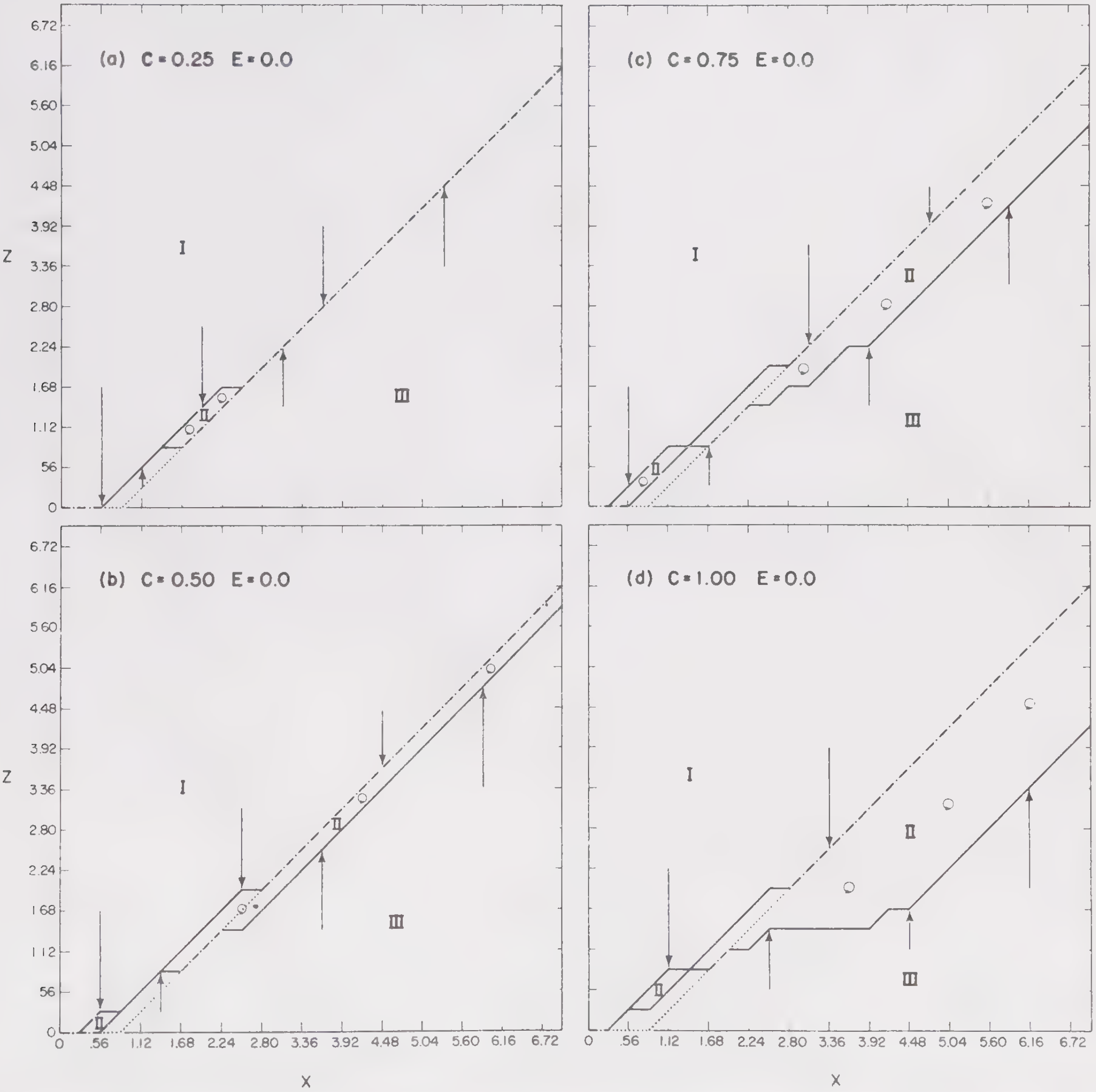

FIGURE 2(a-m).—Optimal policy functions for the Wood River for various assumptions about the relative value of smoothing costs. (See text for details).

7) Base stock size of 0.2 till 0.6, then a base stock size of 0.4.
8) Base stock size of 0.2 till 1.0, then a base stock size of 0.4.
9) Base stock size of 0.2 till 0.4, base stock size of 0.4 till 1.2, base stock size of 0.6 after that.

These nine approximate policies were devised by examining the functions that define the three regions in Figures 2 and 3. These approximate the boundaries of the three regions where the smoothing costs are one-fourth to one-half the per unit value of the harvest. The mean per period harvest, variance, standard deviation, median per period harvest, etc. for these nine policies are given in Table 2.

Policies 3 and 4 for the Wood River and 8 and 9 for the Branch River demonstrate how these approximate policies tend toward smoothing policies. For example, policy 4 has the same median harvest as the optimal base stock harvest, almost never closes the fishery, significantly de-

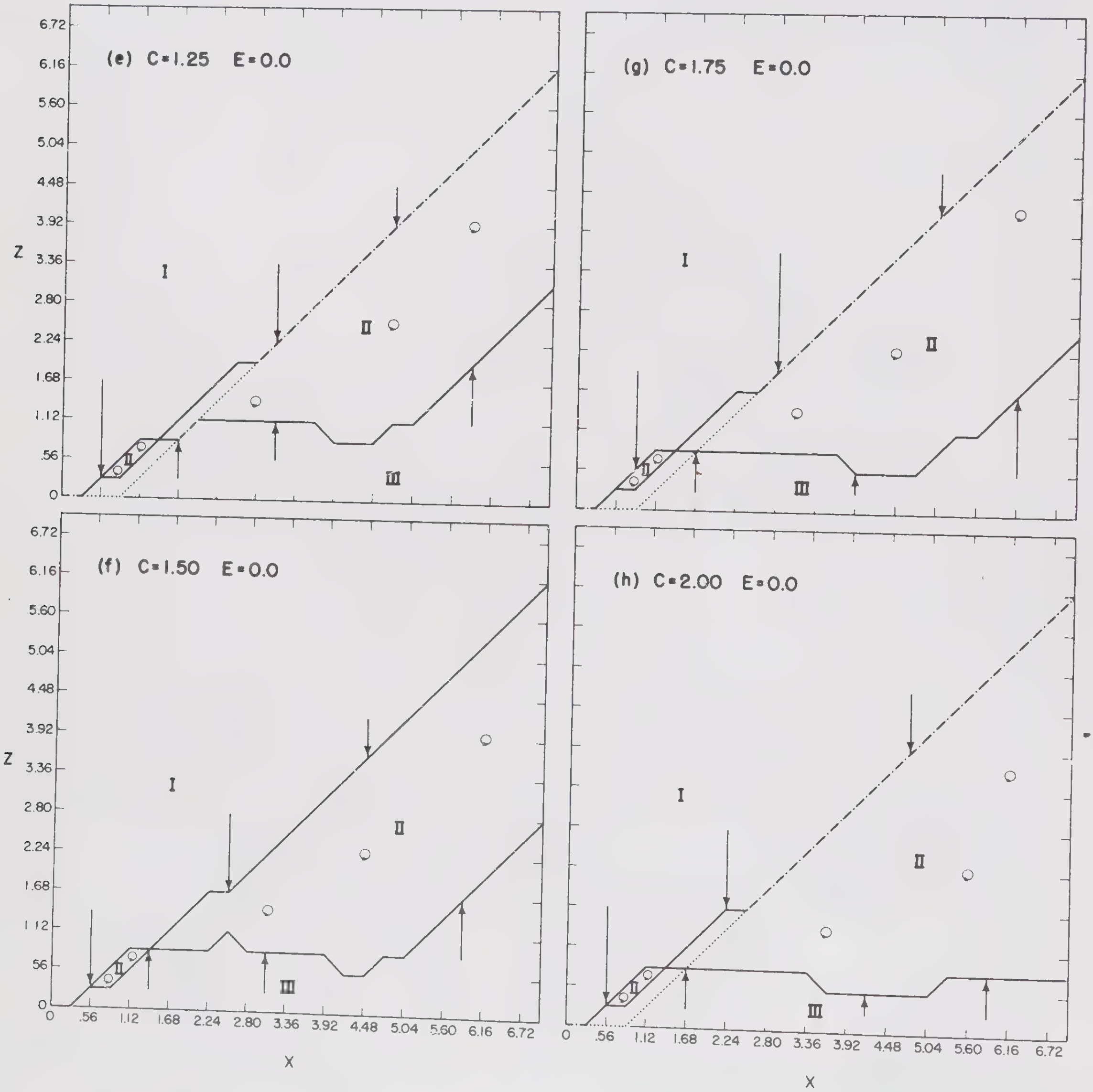

FIGURE 2.—Continued.

creases the percent of time there are low catches, and only reduces the mean per period harvest by 33,800 fish. In order to achieve a smoother catch, "potlatch" harvests from time to time have been sacrificed.

When looked at closely, these policies are actually very intuitive and represent an interesting variant of a base stock policy. These policies replace a single base stock size by a dual base stock size policy. The first base stock size is lower than the original one, while the second base stock size is greater than or equal to the original base stock size. This means that there are fewer states where there is no harvesting, but also lowers the likelihood of the really big harvests. The mean per period harvest tends to be very sensitive to these big harvests, while the median is not, particularly since the very large harvests are not too frequent.

It is curious that the population dynamics are so sensitive to such fine tuning, for the difference between policy 1 and policy 3, say, is quite marginal. It would be an interesting area of future

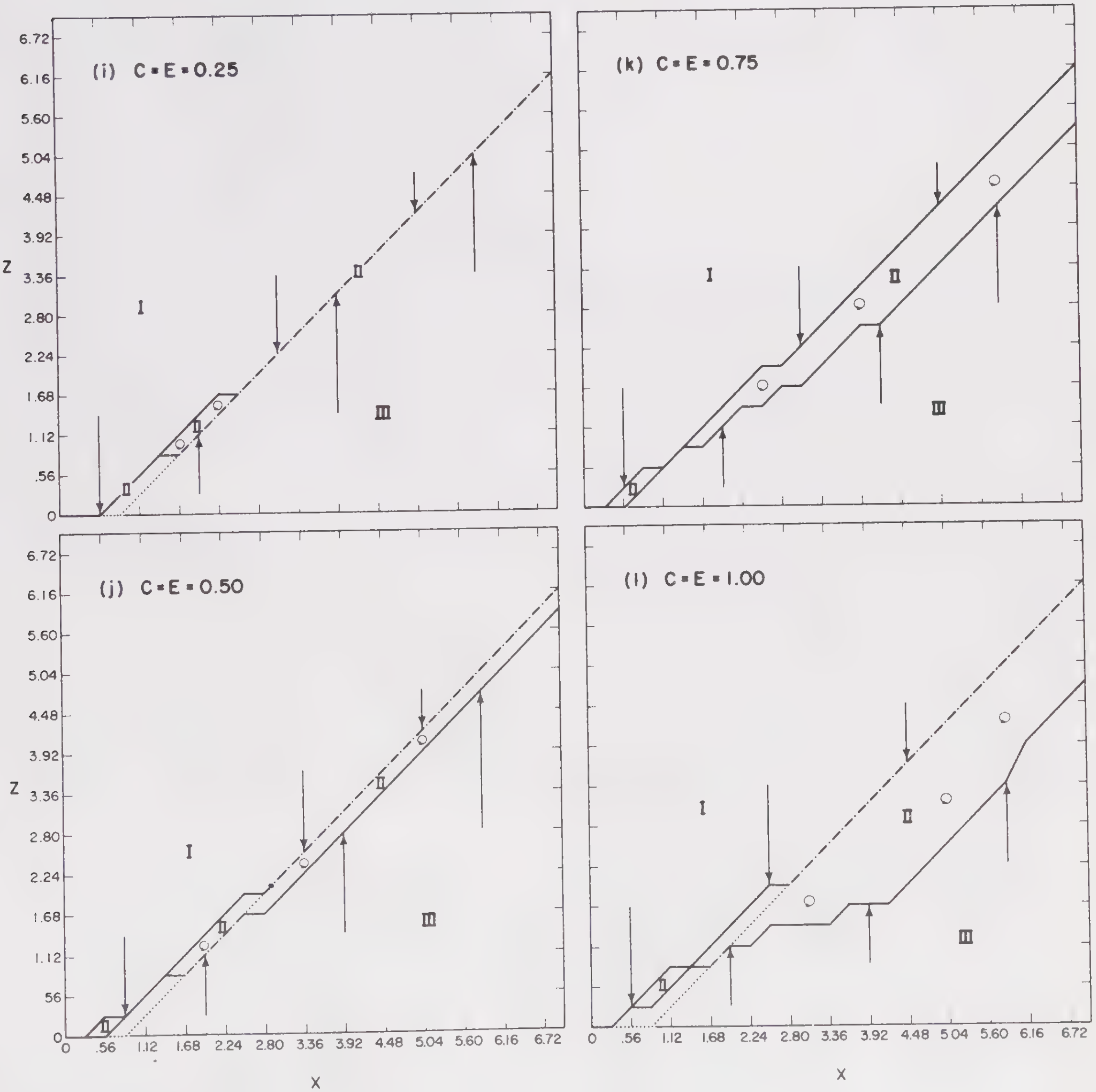

FIGURE 2.—Continued.

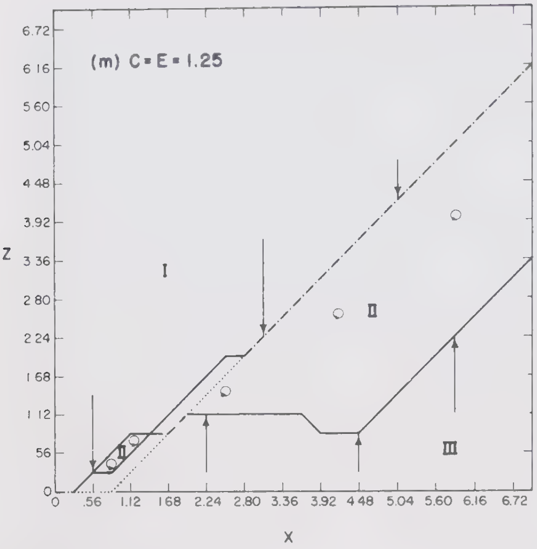

FIGURE 2.—Continued.

research to determine guidelines for when fine tuning would be expected to produce such "trimming" of the tails of the ergodic (long-run probability) distribution.

Including smoothing costs also tells us a great deal about traditional concepts of fisheries management, such as MSY. It is clear from Figures 2 and 3 that anything close to an MSY policy is optimal only if the smoothing costs exceed the per unit value of the harvest. As whole systems of laws for regulating fisheries have been constructed around the idea of smooth, constant harvests, it is clear that this imputes lower average catches, and a significant preference for constancy of the harvest over total amount harvested.

The analysis has assumed that Equation (1.1) or similar equations are available, and that the parameter estimates are accurate (in this case, estimates of R_1, R_2, and σ^2). In the latter case, management measures would seem more reasonable if they were known to be robust against misspecifying the parameters. This involves knowing how an optimal policy and total expected value would vary if the true underlying parameter values differ from those specified, and also how the estimate of the long-run probability distribution differs from the true one.

Walters and Hilborn (1976) have examined a similar question of trying to solve the Bayes model of this problem, i.e., where there is an original prior probability given to each value of the parameter, and this probability is updated each period using Bayes theorem and the observed values during the period. However, they could not obtain a solution, and Walters and Hilborn (1978) raised questions as to the validity of some of their numerical approximations.

Fortunately, qualitative results are possible for this particular class of Bayes problems. Let Θ be the parameter (or vector of parameters) under consideration. Let $q_0(\Theta)$ be the initial prior distribution on Θ, and let $q_n(\Theta)$ be the updated prior distribution after n period has elapsed. Let Ω be the set of all possible prior distributions. Then it is proven in van Hee (1977a) that if the state of the system is expanded to (x_t, q_t), the resulting optimization problem is Markovian. Following arguments similar to those in Scarf (1959) and van Hee (1977a) it follows that an optimal Bayes policy takes the form:

For each element $q \in \Omega$, there is an $x(q)$ such that:

do not harvest if $x_t \leq x(q)$

harvest $x_t - x(q)$ if $x_t > x(q)$.

For example, if σ^2 in the distribution of d is itself a random variable, then each possible probability distribution of σ^2 yields a possibly unique base stock size policy.

TABLE 2.—Vital statistics for the nine policies approximating the smoothing cost policies for Wood and Branch Rivers.

River	Policy	Mean per period harvest	Variance of per period harvest	Standard deviation	% time no catch	% time less than 25% of mean	% time greater than mean catch	Median catch	Relative value: smoothing/price
Wood	1	1.1357	0.8468	0.9202	5.6	16.8	39	0.98	0/1
	2	1.0993	0.5460	0.7389	1.7	10.7	39.8	0.98	1/8
	3	1.1203	0.6506	0.8066	1.1	7.7	43.2	0.91	1/4
	4	1.1019	0.5758	0.7588	0.02	10.47	40	0.98	1/2
Branch	5	0.6528	0.3982	0.6310	9.2	21.8	40	0.500	0/1
	6	0.6290	02532	0.5032	9.1	21.5	37.2	0.500	1/4
	7	0.6272	0.3077	0.5547	1.2	27.7	31.3	0.400	1/2
	8	0.5920	0.2202	0.4693	1.9	35.7	26.3	0.500	3/8
	9	0.5995	0.3038	0.5512	0.72	22.83	39.3	0.500	3/4

Van Hee (1977a) defined a set of policies that he terms Bayes equivalent policies. For problems such as the salmon models under discussion, a Bayes equivalent policy would be found as follows:

1) At the start of the period, the prior probability distribution is $q(\Theta)$.

2) The expected transition function (expectation with respect to Θ) is calculated, i.e.,

$$p(d, q) = \int p(d \mid \Theta) q(d\Theta) \qquad (4.1)$$

where $p(\cdot \mid \cdot)$ describes the dependence of the random variable d on Θ.

3) $p(d, q)$ is used to solve a non-Bayesian Markov decision process, with $p(d, q)$ as the transition function.

4) The optimal policy from step 3 above is used for one period.

5) $q(\Theta)$ is updated using Bayes theorem and the observations from the last period, and the updated $q(\cdot)$ is used in step 1 at the next time period.

It is worth noting that a Bayes eqivalent policy

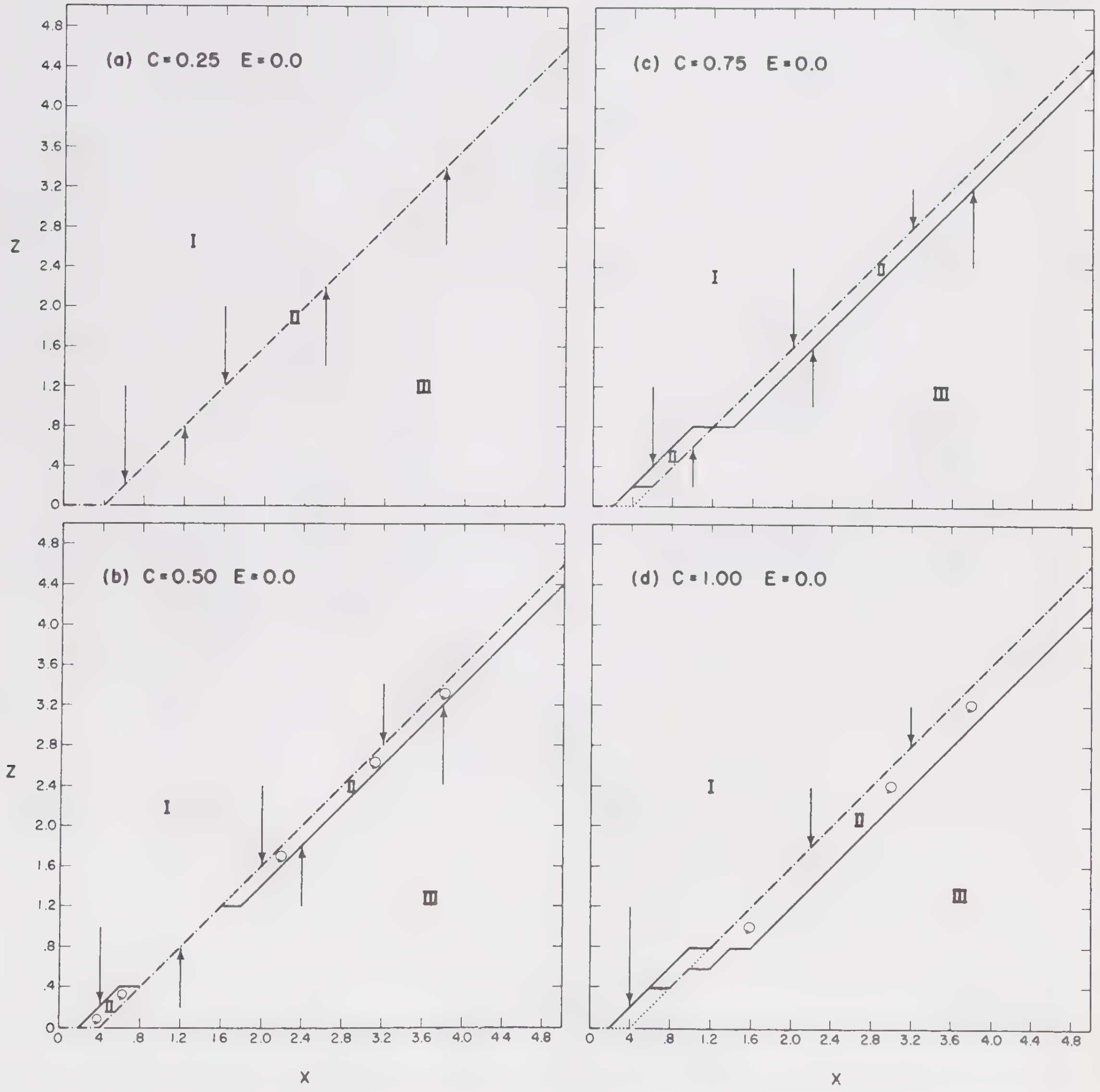

FIGURE 3(a-m).—Optimal policy functions for the Branch River for various assumptions about the relative value of smoothing costs. (See text for details.)

is adaptive, as the prior distribution is updated each period. Moreover, it is not the same as fixing Θ at its estimated value, and using a fixed value of Θ in step 3. The difference can be seen in the integral in Equation (4.1). The reason for considering Bayes equivalent policies is that van Hee (1977a, theorem 3.1) proved that for the models under discussion, when the objective is given by Equation (1.2a) or (1.2b), then the Bayes equivalent policy is optimal for the full Bayes model. For example, in Walters and Hilborn (1976), the parameter Θ is a scalar, i.e., R_2 in our notation. Their problem, for which an optimal policy was not found, can be solved by following a policy outlined in the five steps above.

Many models will not have the necessary structure for a Bayes equivalent policy to be optimal for the full Bayes model, and unlike salmon management, estimates of the population size may not be available every year. A legitimate question is: suppose the present best estimate of Θ were to be used from hereafter. What would be the loss in

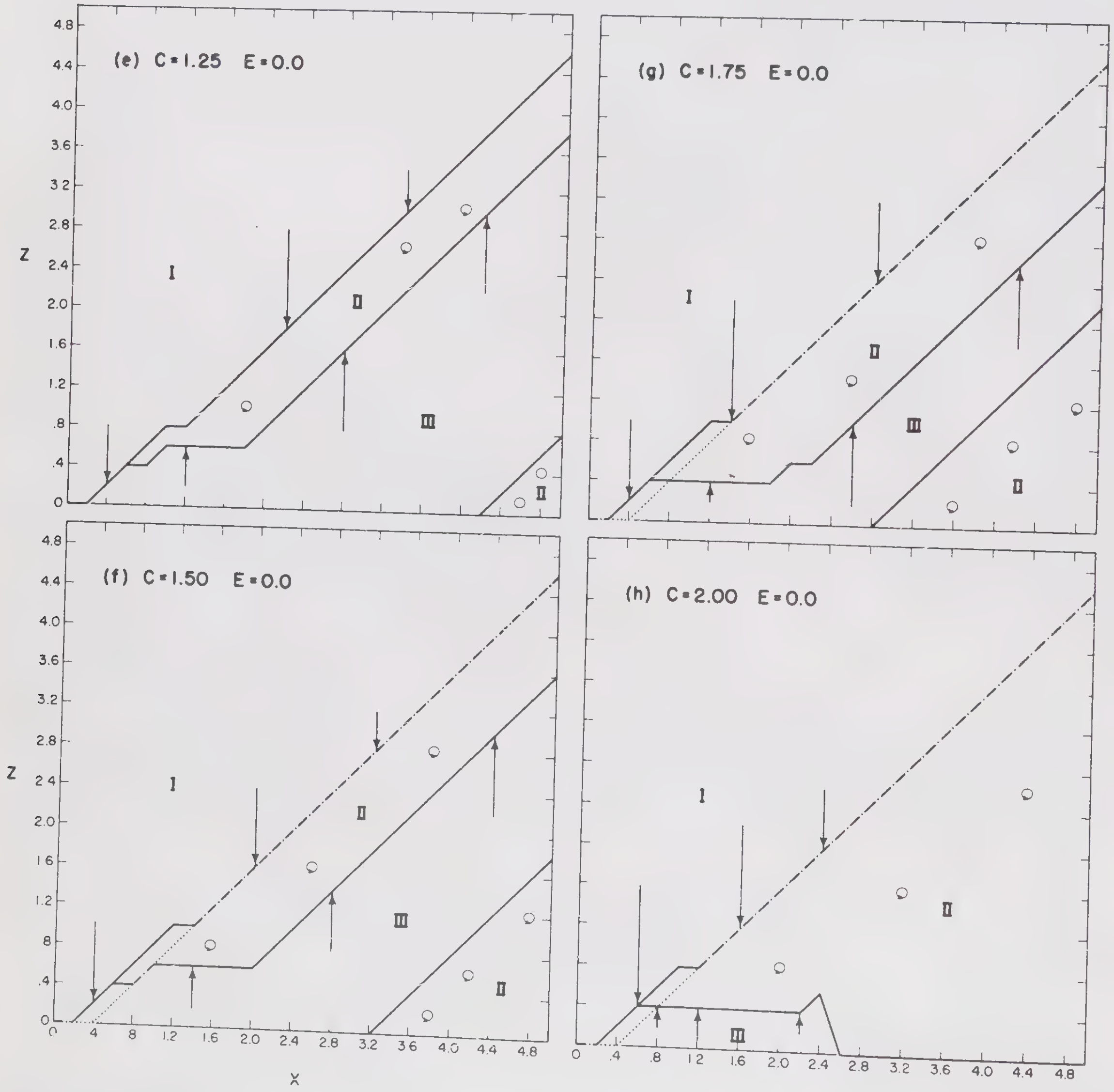

FIGURE 3.—Continued.

expected value? Van Hee (1977b) gave bounds on this expected loss that are easy to compute. To obtain a feel for these bounds, both σ^2 and R_2 are assumed to be random variables. For the Wood River, R_2 could take on the values -0.6, -0.8 and -1.0, and for the Branch River R_2 could take on the values -1.5, -1.85, and -2.00. For the Wood River, σ^2 could assume the values of 0.35, 0.45, and 0.55, and for the Branch River σ^2 could assume the values 0.48, 0.58, and 0.68. Three probability distributions were used as the present prior probability of the parameter values. These were (⅓, ⅓, ⅓,), (¼, ½, ¼), (⅛, ¾, ⅛). The results of the optimization using the parameters at each fixed value (which are needed to calculate the bounds) are given in Table 3. Table 4 gives the bounds on the expected loss of value from using the present estimates of the parameters as in Equation (1.1).

Table 3 suggests that as σ^2 varies for fixed values of R_1, R_2, the mean per period harvest varies little, but the variance of the long-term harvest size distribution increases significantly. As R_2

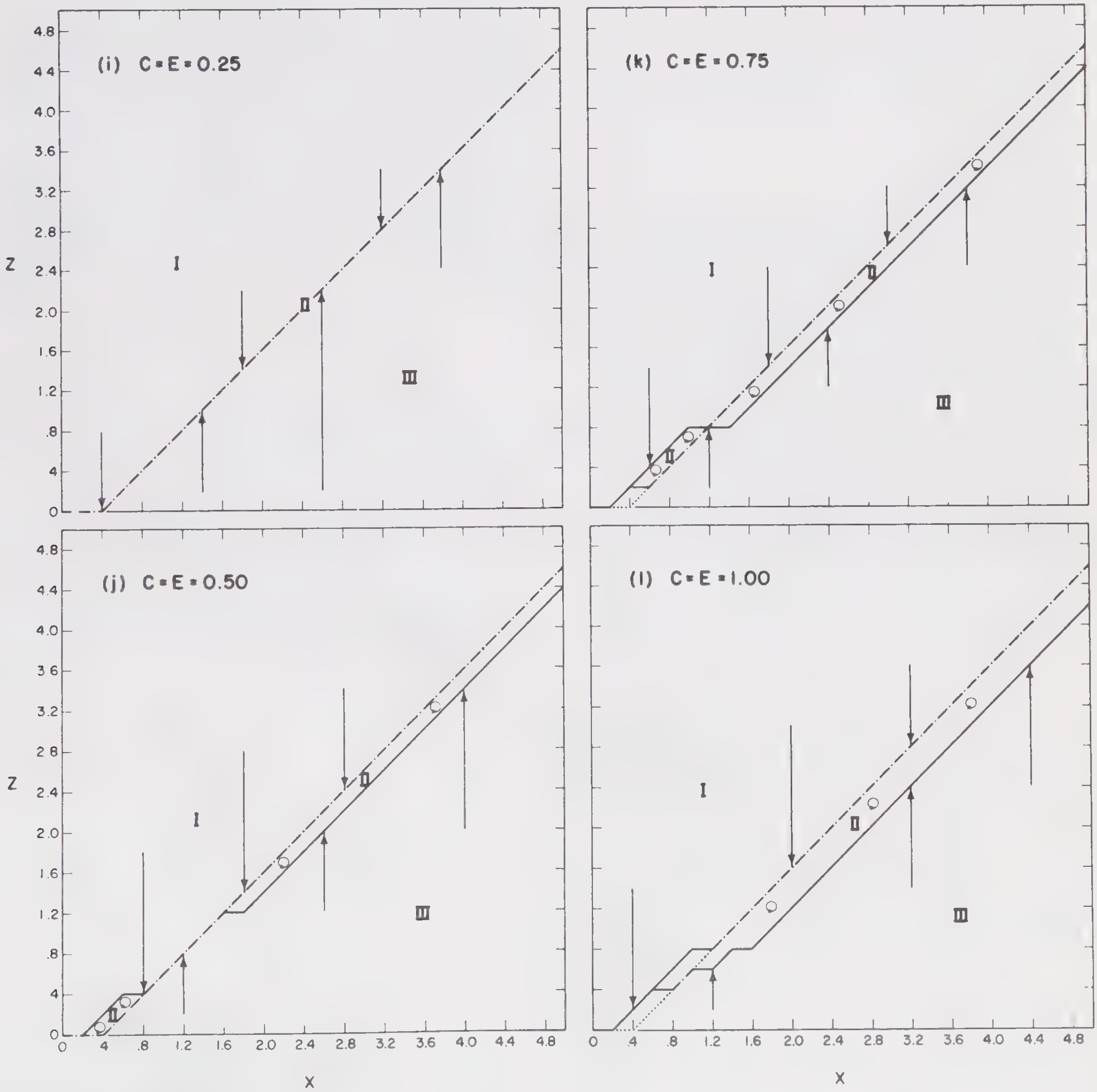

FIGURE 3.—Continued.

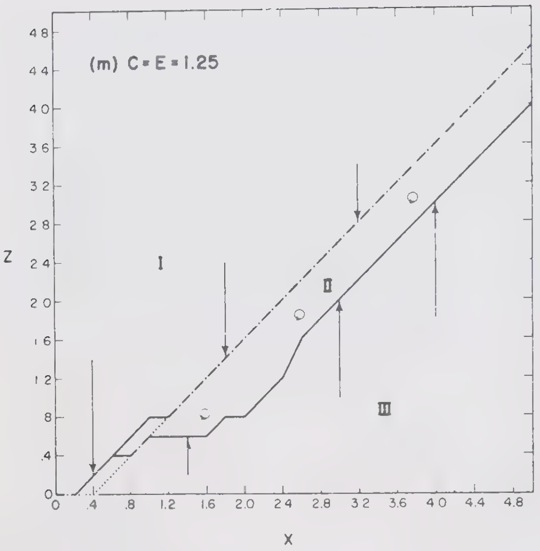

FIGURE 3.—Continued.

varies for fixed values of R_1, σ^2, both the mean and the variance vary significantly. Table 4 reinforces this impression to a degree. If the mean per period harvest does not vary significantly with changes in the value of σ^2, it might be expected that the present estimate of σ^2 will suffice. This is borne out by Table 4, where the bounds on the maximum expected total loss is <0.01, which is <1% of the optimal Bayes expected value.

Some significant expected loss in value when R_2 varies is seen, but the loss is less than might be expected from Table 3. The values in Table 4 when R_2 varies are all <4% of the true value. These results suggest that if Equation (1.1) is the correct form of the model, and the present parameter estimates have relatively small variance, then little is gained in expected value if the more complicated policy is used. The same may not be true if the population size is unobserved.

All of these results suggest a model that is fairly robust to our lack of understanding of nature. A possible explanation for this can be made from the discussion on the effect of grid size. As long as there is some cutoff population size below which no harvesting is allowed, and this cutoff assures that the absorbing state cannot be reached with probability one, then our management can only damage the stocks to a degree.

All of the policies examined in this paper have such a minimum cutoff. The rest of the policy will determine the relative mean and variance of the harvest, and techniques are presented to examine these features in detail. Uncertainty about the values of the parameters will affect the total return, but present estimates often can give a satisfactory approximation. The truly risk adverse decision maker can use present estimates of the parameters that are weighted to be on the cautious side.

SUMMARY

Uncertainty in fisheries management can be faced head on. Techniques exist that allow us to gain much insight on managing randomly varying populations. Optimization procedures allow us to reduce our attention to the few best policies, and to analyze their properties, rather than to pick policies ad hoc that meet no special criteria.

Optimization under uncertainty can also lead to a reconsideration of what is valued in managing a

TABLE 3.—Trials with varied parameters.

River	Value of R_2	Value of σ	Optimal policy	Mean per period harvest	Variance	% time no harvest
Wood	-0.800	0.35	min (x_t, 0.7)	1.0680	0.390976	0.79
Wood	-0.800	0.55	min (x_t, 0.77)	1.2267	1.2422	7.8
Wood	-0.600	0.458	min (x_t, 0.980)	1.5108	1.3136	3.8
Wood	-1.000	0.458	min (x_t, 0.560)	0.9225	0.4839	3.29
Branch	-1.845	0.48	min (x_t, 0.35)	0.6122	0.2253	3.54
Branch	-1.845	0.68	min (x_t, 0.35)	—	—	—
Branch	-1.500	0.579	min (x_t, 0.40)	1.989	0.5254	5.82
Branch	-2.000	0.579	min (x_t, 0.30)	0.9075	0.3068	5.82

TABLE 4.—Largest possible deviation in value of the approximate policy compared with the true Bayes policy.

Probability distribution	When R_2 is uncertain			When σ is uncertain		
	⅓, ⅓, ⅓	¼, ½, ¼	⅛, ¾, ⅛	⅓, ⅓, ⅓	¼, ½, ¼	⅛, ¾, ⅛
Wood River	1.4	0.51	0.5	0.04	0.03	0.03
Branch River	1.04	0.47	0.38	0.01	≤0.01	≤0.01

fishery—in the examples considered, some consistency in the amount harvested is a desirable alternative to high year-to-year fluctuations in the harvest size. But this reduced the average per period catch. Only in extreme situations, where the cost of smoothing out the catch is greater than the unit value of the catch, does any policy resembling MSY become optimal.

Finally, it is possible to obtain an understanding of how robust the management measures are to misspecifications of the underlying model. This is important, since the model is only a guide to our decision making, not the answer. In the models considered, the "best" policies are robust in view of this uncertainty.

A question not examined is the assumption that the population size is observed at the start of each period. This too is usually costly, and inexact. Recently, I and E. J. Sondik developed an efficient algorithm that addresses the relative merits of different sampling intervals for obtaining population estimates.[5] Together, all of these techniques allow for an integrated, realistic approach to management under uncertainty.

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Notes, Comments, and Letters to the Editor

Capital Accumulation and the Optimization of Renewable Resource Models*

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1. INTRODUCTION

There are separate literatures on normative models of capital accumulation, fisheries management, and reservoir operation. However, generic models of each type share a common mathematical structure. The models often include uncertainty in the length of time to which planning should apply and in the future consequences of present decisions.

The present paper investigates the structure of optimal decision making under uncertainty for general single sector growth models, for individual optimal consumption and savings models, for models of a single fish species with pooled age classes, and for models of a single reservoir. The results extend and unify some of those of Amir (1967), Bewley (1977), Levhari and Srinvinasan (1969), Hakaanson (1970), Mirman (1971), Brock and Mirman (1972, 1973), Miller (1974), Sobel (1975), Whitt (1975a), Schechtman (1976), Schechtman and Escudero (1977), and Yaari (1976). Also we present new and simpler proofs for most of the theorems which generalize results of the authors above.

For brevity, we use the terminology of capital accumulation. Let the first consumption and reinvestment decisions be made in period n and the last

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ones in period 1. At the beginning of each period t ($t = 1, 2, \ldots$) let x_t denote the capital on hand in units of dollars or physical quantities as the context dictates. The decisions in period t are y_t, namely the amount of x_t that is reinvested, and $z_t = x_t - y_t$, the amount consumed. Let

$$y_t \in Y(x_t) \qquad (t = 1, 2, \ldots) \tag{1.1}$$

constrain the reinvestment and consumption decisions. The connection between reinvestment decisions and accumulated capital is

$$x_{t+1} = s(y_t, D_t), \tag{1.2}$$

where $D_1, D_2, \ldots, D_n$ are assumed to be independent random variables that are distributed as the generic random variable D. We assume for each t that x_t lies in a convex reference set X and that $C \equiv \{(x, y): y \in Y(x), x \in X\}$ is a convex set.

Let $G(x_t, y_t)$ denote the utility in period t of having an initial capital x_t and reinvesting y_t. Let α denote the single-period discount factor. The generic problem is maximization of expected discounted utility, namely $E \sum_{t=1}^{n} \alpha^{t-1} G(x_t, y_t)$, where $n \leqslant \infty$. With a *consumption horizon* of n periods until termination, let $A_n(x)$ denote an optimal reinvestment decision and $x - A_n(x)$ an optimal consumption decision. (For a fishery model, $x - A_n(x)$ is the amount harvested, and $A_n(x)$ is the population size after harvesting ceases. For a reservoir model, x is the amount of water in the reservoir, and $x - A_n(x)$ is the amount discharged.)

The real line is indicated by $\mathbf{R}$, and $\mathbf{R}_+$ denotes $[0, \infty)$. If $z \in \mathbf{R}$ then $(z)^+$ denotes $\max(0, z)$. Derivatives (partial or regular) are from the left when necessary. If $w(\cdot, \cdot)$ is a function of two variables, then $w^{(1)}(u, v)$ and $w^{(2)}(u, v)$ denote the partial derivatives with respect to the first and second arguments. If $a \in \mathbf{R}$ and $b \in \mathbf{R}$, then $a \wedge b$ denotes $\min(a, b)$.

Suppose w is a real-valued concave function on $\mathbf{R}$ and D is a random variable for which the expectations $r(z) \equiv Ew(z - D)$ and $Ew'(z - D)$ both exist. Then $r'(z) = Ew'(z - D)$ can be justified by the monotonicity in δ of $[w(z - D) - w(z - D - \delta)]/\delta$ (because w is concave) and the Dominated Convergence Theorem (Royden 1963).

2. New Features of the Model

The results in this paper relax the assumptions of the previously cited papers in five important ways. First, many of our results do not assume that single-period utility depends only on consumption, that is $G(x, y) \equiv g(x - y)$. In renewable resource models, the benefits of a harvest $x_t - y_t$ are offset by harvesting costs that typically depend separately on the stock size x_t and the amount harvested $x_t - y_t$.

Second, when the utility function does depend only on consumption, we assume neither $g'(0) = +\infty$ nor strict concavity of $g(\cdot)$. Neither assumption is salient for many renewable resource models. However, one or both of the assumptions is found in most of the cited references, most particularly Bewley (1977), Brock and Mirman (1972), Mirman and Zilcha (1975), and Schechtman (1976). Thus their models fail to encompass either linear utilities or quadratic utilities, or both. These cases are empirically useful.

Third, we avoid assumptions about $s(\cdot, \cdot)$ (in (1.2)) that would block applications to renewable resource models. The Inada condition

$$s^{[1]}(0, \cdot) \equiv +\infty, \qquad s^{[1]}(\infty, \cdot) \equiv 0$$

are not imposed. Note that the simple case $s(y, d) = \rho y + d$ violates the Inada condition as do quadratic functions. For several of the results it is not assumed that $s(\cdot, d)$ is nondecreasing for each fixed value d of D_t. We avoid continuity and ordering assumptions about $s(y, \cdot)$ such as are found in Brock and Mirman (1972), Schechtman (1976), and Bewley (1977). When $G(x, y) = p \cdot (x - y)$, new results are presented that assume only pseudoconcavity of $s(\cdot, d)$ for each fixed value d of D_t. This last assumption is often made in models of renewable resources.

Fourth, *effective constraints* are allowed in the model. We do not assume existence of interior solutions. In renewable resource models, the absence of Inada conditions typically causes some constraints to be active at an optimum. This makes the analysis more complex because it is no longar possible to assume that the derivative of an optimal value function equals $g'(x, x - A_n(x))$. The methods of proof, therefore, differ significantly from those in previously cited papers.

Finally, a unified treatment is presented for both the finite and infinite horizon problems. Our proof that the infinite horizon optimal policy $A(x)$ is the limit of the $A_n(x)$'s is more straightforward than those of Schechtman and Escudero (1977) (who assume $s(y_t, D_t) = \rho y_t + D_t$) and Brock and Mirman (1972) (who assume strict concavity, interior solutions and impose other restrictive conditions) although our model is sufficiently general to encompass renewable resource applications.

Also, we present a straightforward short proof that a unique stationary distribution of wealth exists. The proof uses a result of Rosenblatt (1967) and is much shorter and simpler than proofs of essentially the same theorem by Brock and Mirman (1972), Brock and Majumdar (1975), and Mirman and Zilcha (1975).

The model in Bewley (1977) is richer probabilistically than ours. Although his model requires $G(x, y) \equiv g(x - y)$ and $s(y, d) \equiv y + d$, g is stochastic with $\{(g_t, D_t)\}$ being a stationary stochastic process.

3. ASSUMPTIONS

The following assumptions are made in various combinations.

(3.1) G is finite, concave, and continuous on C;

(3.2) for each y, $G(\cdot, y)$ is nondecreasing on $\{x: (x, y) \in C\}$;

(3.3) $G(x, y+\gamma) - G(x, y) \leqslant G(x+\lambda, y+\gamma) - G(x+\lambda, y)$ for all $\gamma > 0$, $\lambda > 0$ with all arguments in C;

(3.4) G is nonnegative and continuous on C;

(3.5) for each d, $s(\cdot, d)$ is continuous and concave on the set $\mathbf{Y} = \bigcup_{x \in X} Y(x)$;

(3.6) for each d, $s(\cdot, d)$ is continuous and concave on the set $[0, y^o(d)]$ and convex on the set $[y^0(d), \infty)$;

(3.7) for each d, $s(\cdot, d)$ is nondecreasing on $\mathbf{Y}$;

(3.8) $G(x, y) = p \cdot (x - y), p \geqslant 0$;

(3.9) $Y(x) = [0, x], x \in X$.

Assumption (3.4) is slightly deceptive because several articles, including Phelps (1962), Hakaason (1970), and Miller (1974), have $G(x, y) = \log(x - y)$, for $x - y \geqslant \xi > 0$. However, nonnegativity of G is equivalent to having a uniform lower bound. Suppose, for example, that $G(x, y) \geqslant -B$ if $(x, y) \in B$ $(B > 0)$, and let $G^*(x, y) = G(x, y) + B$. Then a policy is optimal with utility function G^* if and only if it is optimal also for G. Moreover, G^* is nonnegative on C. Assumption (3.3) is equivalent to *supermodularity* of G on C. Topkis (1978) discusses supermodularity and its consequences for optimization.

4. OPTIMAL POLICIES

From standard dynamic programming arguments, the generic problem of maximizing $E \sum_{t=1}^{\infty} \alpha^{t-1} G(x_t, y_t)$ leads to the recursion

$$f_n(x) = \sup\{J_n(x, y): y \in Y(x)\}, \qquad x \in X, \tag{4.1}$$

$$J_n(x, y) = G(x, y) + \alpha E f_{n-1}(s[y, D]), \qquad y \in Y(x), \quad x \in X \tag{4.2}$$

for $n = 1, 2,\ldots$ with $f_0(\cdot) \equiv 0$. The proofs of most results will exploit the following diminishing returns property of $f_n(\cdot)$.

THEOREM 4.1. *Assumptions* (3.1), (3.2), (3.5), *and* (3.9) *imply for each* n *that* $f_n(\cdot)$ *is continuous, concave, and nondecreasing on* X.

Proof. The proof that $f_n(\cdot)$ inherits concavity and is nondecreasing is ell known and will not be reproved. Our proof of continuity is new and impler than related proofs in Brock and Mirman (1972) and Schechtman 1976).

Let p be a metric on the space in which X lies. To initiate a contrapositive roof, suppose f_n experiences a discontinuity at $x^0 \in X$. Then there is a $^0 \in Y(x^0)$ and a real number $\gamma > 0$ with the property that for all real umbers $\delta > 0$ there exists $x \in X$ such that

$$p(x, x^0) < \delta \qquad \text{and} \qquad J_n(x, y) \geqslant \gamma + J_n(x^o, y^o), \qquad y \in Y(x). \quad (4.3)$$

Concavity precludes the reverse inequality for J). Because C is a convex set is possible to select a subsequence (x^j, y^j) satisfying (4.3) and $(x^j, y^j) \rightarrow$ $x^0, y^0)$. Therefore, contrary to assumption, J_n is discontinuous at (x^0, y^0). ∎

Continuity of $J_n(x, \cdot)$ on $Y(x)$ for each $x \in X$ follows from (3.1), (3.5), nd continuity of $f_{n-1}(\cdot)$ via Theorem 4.1. Compactness of $Y(x)$ via (3.9), herefore, implies attainment of the supremum in (4.1) for each $x \in X$ and xistence of an optimal policy.

The next two theorems describe the dependence of $A_n(x)$ on x. They lead n Corollary 4.2) to sufficient conditions for $0 \leqslant dA_n(x)/dx \leqslant 1$. Many uthors have proved at least one side of this inequality for special cases of ur model.

THEOREM 4.2. *Assumptions* (3.1)–(3.3), (3.5), *and* (3.9) *imply for each* n *hat there exists* $A_n(\cdot)$ *with the property*

$$A_n(x') \geqslant A_n(x) \qquad \text{if} \quad x' \geqslant x. \qquad (4.4)$$

Proof. The theorem would be true if, for $\delta > 0$,

$$J_n(x', A_n(x)) - J_n(x', A_n(x) - \delta) \geqslant J_n(x, A_n(x)) - J_n(x, A_n(x) - \delta) \geqslant 0.$$

he right inequality is implied by the optimality of $A_n(x)$. The left inequality ould be implied by $J_n^{[21]}(\cdot, y)$ being nondecreasing on $\{x\colon (x, y) \in C\}$. From 4.2),

$$J_n^{[21]}(x, y) = G^{[21]}(x, y) + \alpha E\{f'_{n-1}(s[y, D])\, s^{[1]}(y, D)\}$$

o (3.3) completes the proof. ∎

Theorem 4.2 requires neither $G(x, y) \equiv g(x - y)$ nor strict concavity. It ssumes concavity of $s(\cdot, d)$ but not monotonicity. Theorem 4.3 obtains a rther result when $G(x, y) \equiv g(x - y)$ and $Y(x) = [0, x]$.

THEOREM 4.3. *Assumptions* (3.1)–(3.3), (3.5), (3.9), *and* $G(x, y) \equiv g(x-y)$ *imply for each* n *that there exists* $A_n(\cdot)$ *with the property*

$$0 \leqslant A_n(x') - A_n(x) \leqslant x' - x \qquad \text{if} \quad x \leqslant x' \tag{4.5}$$

Proof. The left inequality is (4.4). To prove the right one, let $z = x - y$ and rewrite (4.1) and (4.2) as

$$f_n(x) = \sup\{H_n(x, z)\colon 0 \leqslant z \leqslant x\}, \qquad x \in X,$$
$$H_n(x, z) = g(z) + \alpha E f_{n-1}(s[x - z, D]).$$

The right side of (4.5) would be valid if

$$\begin{aligned} 0 &\leqslant H_n^{[2]}(x+\delta, z) - H_n^{[2]}(x, z) \\ &= \alpha E\{f'_{n-1}(s[x - z, D])\, s^{[1]}(x - z, D) \\ &\quad - f'_{n-1}(s[x + \delta - z, D])\, s^{[1]}(x + \delta - z, D)\} \end{aligned} \tag{4.6}$$

for $\delta > 0$ as will be shown.

Concavity of $s(\cdot, d)$ implies

$$s^{[1]}(x + \delta - z, d) \leqslant s^{[1]}(x - z, d).$$

If $s^{[1]}(x + \delta - z, d) \geqslant 0$ then concavity implies $s(x - z, d) \leqslant s(x + \delta - z, d)$ so $0 \geqslant f'(s[x + \delta - z, d]) \leqslant f'(s[x - z, d])$ and

$$f_{n-1}(s[x + \delta - z, d])\, s^{[1]}(x + \delta - z, d) \leqslant f_{n-1}(s[x - z, d])\, s^{[1]}(x - z, d). \tag{4.7}$$

If $s^{[1]}(x + \delta - z, d) < 0 \leqslant s^{[1]}(x - z, d)$ then (4.7) is trivial. If $0 > s^{[1]}(x - z, d) \geqslant s^{[1]}(x - z + \delta, d)$ then $s(x - z, d) \geqslant s(x + \delta - z, d)$ because $s(\cdot, d)$ is concave. Concavity and monotonicity of $f_{n-1}(\cdot)$ and these inequalities yield

$$0 \leqslant f'_{n-1}(s[x - z, d]) \leqslant f'_{n-1}(s[x + \delta - z, d]),$$
$$0 > s^{[1]}(x - z, d) \geqslant s^{[1]}(x + \delta - z, d)$$

and, therefore, (4.7), which proves (4.6). ▮

COROLLARY 4.1. *The assumptions of Theorem* 4.3 *and* $0 < A_n(x') < x'$ *for some* $x' > 0$ *imply* $0 < A_n(x)$ *for all* $x \geqslant x'$.

COROLLARY 4.2. *The assumptions of Theorem* 4.3 *imply*

$$0 \leqslant dA_n(x)/dx \leqslant 1, \qquad x \in X^0, \tag{4.8}$$

where X^0 *denotes the interior of* X.

Proof. From Theorem 4.4, $A_n(\cdot)$ is nondecreasing so its discontinuities, if any, are upward jumps. These jumps are precluded by $A_n(x) - x$ being nonincreasing so $A_n(\cdot)$ is continuous. Monotonicity of $A_n(\cdot)$ implies differentiability except, possibly, on a set of measure zero where one-sided derivatives exist, so (4.6) implies (4.8). ∎

Corollary 4.2 treats a more general problem than Schechtman (1976) does and its proof seems more straightforward.

An optimal policy, $A_n(x)$ can be described in further detail if $Y(x) = [0, x]$ and $G(x, y) = p \cdot (x - y)$ for $p \geqslant 0$. After substitution and rearrangement of terms, the optimization problem becomes:

$$\text{maximize } E\left\{px_1 - \alpha^{T-1}y_T + p\sum_{t=1}^{T} \alpha^{t-1}(\alpha s[y_t, D_t] - y_t)\right\}$$

subject to $0 \leqslant y_t \leqslant x_t$, $t = 1, \ldots, T$. The first term, px_1, is fixed. The second term, $-\alpha^{t-1}y_T$, has $y_T \equiv 0$ for an optimal policy (if $\alpha > 0$). Therefore, an equivalent problem, in the sense of having the same optimal policy for all $n > 1$, is given by the following recursion:

$$f_0(\cdot) \equiv 0,$$

$$f_n(x) = \sup\{J_n(y) \colon 0 \leqslant y \leqslant x\},$$

where $J_n(y) = G(y) + \alpha E f_{n-1}(s[y, D])$ and $G(y) = p \cdot (\alpha E s[y, D] - y)$.

Let x_n^0 denote a global maximum of $J_n(y)$. For $x_n \geqslant x_n^0$, it is optimal to consume $x_n - x_n^0$. If $J_n(\cdot)$ is pseudoconcave for all n, then it is straightforward to prove that an optimal policy is given by:

$$A_n(x) = x \wedge x_n^0.$$

What conditions ensure pseudoconcavity of $J_n(y)$? Corollary 4.3 is an immediate extension of Theorem 4.1.

COROLLARY 4.3. *Assumptions* (3.4), (3.5), (3.8), *and* (3.9), *imply*:

(i) $J_n(y)$ *is concave and continuous,*

(ii) $A_n(x) = x \wedge x_n^0$. ∎

Suppose

$$s(y, d) = d\phi(y), \qquad P\{D \geqslant 0\} = 1, \tag{4.9}$$

and

$\phi(\cdot)$ *is pseudoconcave and continuous with mode at* y_m.

When both (3.6) and (4.9) are valid, $y^0(\cdot) \equiv y^0 \geqslant y_m$.

THEOREM 4.4. *Assumptions* (3.6), (3.9) *and* (4.9) *imply*

$$A_n(x) = x \wedge x_n^0$$

is optimal.

Proof. Let $\mu = E(D)$. At $n = 1$, $x_1^0 = \inf\{y: \phi'(y) \leqslant (\alpha\mu)^{-1}\} \leqslant y^m \leqslant y^0$. We use $f_0(\cdot) \equiv 0$. The inductive assumption is that $f_{n-1}(\cdot)$ is concave nondecreasing on X. In

$$J_n'(y) = p(\alpha\mu\phi'[y] - 1) + \alpha\phi'(y)\, E(Df_{n-1}'[D\phi(y)]),$$

the first term is nonpositive if $y \geqslant y^m \geqslant x_1^0$ and the second term is nonpositive if $y \geqslant y^m$ because then $\phi'(y) \leqslant 0$ (while $f'(\cdot) \geqslant 0$ and $P\{D \geqslant 0\} = 1$). Therefore, $x_n^0 \leqslant y^m$ so $A_n(x) = x \wedge x_n^0$ and $f_n(x) = J_n(x \wedge x_n^0)$. It follows that $f_n(\cdot)$ is concave nondecreasing if $J_n(\cdot)$ is concave on $[0, x_n^0]$, which is now verified.

$$J_n(y) = p(\alpha\mu\phi[y] - y) + \alpha E(f_{n-1}[D\phi(y)]),$$

whose first term is concave on $[0, x_n^0]$ because $\phi(\cdot)$ is concave on $[0, y^0]$ and $x_n^0 \leqslant y^m \leqslant y^0$. Concavity of the second term is implied by the inductive assumption, $\phi(y)$ being concave nondecreasing on $[0, x_n^0]$, and $P\{D \geqslant 0\} = 1$. ∎

Theorem 4.4 shows that, if $s(y, d) = d\phi(y)$, the shape of $\phi(\cdot)$ beyond its mode doesn't effect an optimal policy in any significant way because an optimal policy always returns the state to the concave part of the curve.

The properties assumed for $s(\cdot, \cdot)$ can be relaxed by making further assumptions about the distribution of D. A stochastic kernel $K(x, y)$ is TP_2 if, for all $x_1 < x_2$ and $y_1 < y_2$, $K(x_1, y_1)\, K(x_2, y_2) \geqslant K(x_2, y_1)\, K(x_1, y_2)$. TP_2 kernels include the exponential and range families of densities which contain the binomial, Poisson, gamma, and normal (with fixed variance) densities.

THEOREM 4.5. *Assumptions* (3.9), (3.8) *with* $p \geqslant 0$, $s(\cdot, d)$ *pseudoconcave and continuous for each* d, *and* D *with a continuous density function that is* TP_2 *implies*:

$$A_n(x) = x \wedge x_n^0.$$

Proof. This theorem and Theorem 4.1 have similar proofs except it must be shown (a) that a convex combination (expectation) of pseudoconcave functions using a random variable with a TP_2 density is again pseudoconcave, and (b) that a nondecreasing nonnegative pseudoconcave function of a pseudoconcave function is again pseudoconcave.

The first claim is Theorem 5.1 of Chapter 3 in Karlin (1968). The second claim is proven here for differentiable functions. From the definition of pseudoconcave functions, $f(\phi[\cdot])$ is pseudoconcave if

$$f'(\phi[y])\,\phi'(y)(y'-y) \leqslant 0 \qquad \text{implies} \quad f(y') \leqslant f(y)$$

First, $f'(\cdot) \geqslant 0$ so the only pertinent case is $\phi'(y)(y'-y) \leqslant 0$. The pseudoconcavity of $\phi(\cdot)$ implies $\phi(y') \leqslant \phi(y)$. However, $f(\cdot)$ is nondecreasing and pseudoconcave, so $f(\phi[y']) \leqslant f(\phi[y])$. ∎

5. EFFECTS OF THE CONSUMPTION HORIZON

This section investigates the impact of the consumption horizon on the structure of an optimal policy and on its valuation. The following result presents sufficient conditions for a longer consumption horizon to induce a higher valuation, greater accumulation, and higher incremental benefits per unit of added capital.

THEOREM 5.5. *For each n and $x \in X$:*

(a) *Assumption* (3.4) *implies*

$$f_n(x) \leqslant f_{n+1}(x); \tag{5.1}$$

(b) *Assumptions*[1] (3.2), (3.3), (3.4), (3.7) *and* (3.9) *imply*

$$A_n(x) \leqslant A_{n+1}(x); \tag{5.2}$$

$$J_n(x, y+\gamma) - J_n(x, y) \leqslant J_{n+1}(x, y+\gamma) - J_{n+1}(x, y), \quad \gamma > 0 \quad \textit{if} \quad (x, y) \in C \quad \textit{and} \quad (x, y+\gamma) \in C; \tag{5.3}$$

$$f_n(x+\gamma) - f_n(x) \leqslant f_{n+1}(x+\gamma) - f_{n+1}(x) \qquad \textit{if} \quad x+\gamma \in X, \quad \gamma > 0. \tag{5.4}$$

Proof. (a) $f_0(\cdot) \equiv 0$ initiates a straightforward inductive proof of (5.1) that uses (3.4).

(b) Observe that (5.3) is supermodularity (cf. Topkins (1978)) of $J_n(x, y)$ in (y, n) for each x, and (5.4) is supermodularity of $f_n(x)$ in (x, n). If $r(a, b)$ is supermodular in (a, b) and $M(\cdot)$ is nondecreasing then $r(a, m[b])$ also is supermodular in (a, b). Hence, *if* $f_{k-1}(x)$ is supermodular in (x, k) for all $k \leqslant n-1$ then (4.2) and (3.7) imply supermodularity of $J_k(x, y)$ in (y, k) for all $k \leqslant n$.

If $J_k(x, y)$ is supermodular in (x, y, k) for all $k \leqslant n$ and if C is a lattice then Theorem 6.2 in Topkis (1978) implies $A_{k-1}(x) \leqslant A_k(x)$ for all $k \leqslant n$. Assumption (3.9) and convexity of X imply that C is a lattice so it remains to establish (5.4).

---

[1] Instead of (3.9) and convexity of X, it is sufficient to assume that $Y(x)$ is a compact lattice for each x, C and X are lattices, and $Y(x)$ is *ascending* on X.

Assumption (3.2) implies $f_1(x+y)-f_1(x) \geqslant 0$ (Theorem 1) so $f_0(\cdot) \equiv 0$ implies (5.4) is valid for $n=0$. Inductively, if (5.4) is valid for all $n \leqslant k-1$ then (5.3) is valid for all $n \leqslant k$. Then Theorem 4.3 in Topkis (1978) implies (5.4) for all $n \leqslant k$. ▮

We are grateful to Donald M. Topkis of Bell Laboratories for suggesting this line of proof. Our earlier version of Theorem 5.1(b) contained superfluous assumptions including concavity of G.

The next result concerns the limiting behavior of f_n and A_n as $n \to \infty$. Suppose

$$0 < \alpha < 1; \tag{5.7}$$

$$G^{[1]}(x, y) < \infty, \qquad (x, y) \in C; \tag{5.8}$$

$$G(x, \cdot) \text{ is nonincreasing on } Y(x), \qquad x \in X; \tag{5.9}$$

let $r_1(x) \equiv x$ and $r_{n+1}(x) \equiv s(r_n(x), D_n)$; then $E \sum_{n=1}^{\infty} \alpha^{n-1} r_n(x) < \infty$. (5.10)

THEOREM 5.2. (a) *Assumptions* (3.1)–(3.5), (3.7), *and* (3.9) *imply for each* $x \in X$ *existence of*

$$A(x) = \lim_{n \to \infty} A_n(x). \tag{5.11}$$

If $G(x, y) \equiv g(x-y)$ *then*

$$0 \leqslant A(x') - A(x) \leqslant x' - x, \qquad x \leqslant x. \tag{5.12}$$

(b) *Assumptions* (3.1), (3.2), (3.4), (3.5), (3.7), (3.9), *and* (5.7)–(5.10) *imply for each* $x \in X$ *existence of*

$$f(x) \equiv \lim_{n \to \infty} f_n(x) \tag{5.13}$$

with $f(\cdot)$ *being concave and nondecreasing on* X.

Proof. (a) From (5.2) $A_n(x) \leqslant A_{n+1}(x) \leqslant x$ for every n and x. Hence, monotone convergence yields (5.11) and, via Theorem 4.3, it yields (5.12).

(b) Optimality of $A_n(x)$, (5.9), (3.7), and $f_{n-1}(\cdot)$ nondecreasing imply

$$\begin{aligned} f_n(x) &= G(x, A_n(x)) + \alpha E f_{n-1}(s[A_n(x), D_n]) \\ &\leqslant G(x, 0) + \alpha E f_{n-1}(s(x, D_n)) \\ &\leqslant \sum_{t=1}^{n} \alpha^{t-1} E G(r_t(x), 0). \end{aligned}$$

Concavity of G implies

$$G(u, v) \leqslant G(u^0, v^0) + [G^{[1]}(u^0, v^0), G^{[2]}(u^0, v^0)] \begin{pmatrix} u - u^0 \\ v - v^0 \end{pmatrix}$$

for all (u^0, v^0) and $(u, v) \in C$. However, $G^{(2)} \leqslant 0$ from (5.9) so

$$\begin{aligned} f_n(x) &\leqslant \sum_{t=1}^{n} \alpha^{t-1} E[G(x, 0) + G^{[1]}(x, 0)(r_t(x) - x)] \\ &\leqslant [G(x, 0) - xG^{[1]}(x, 0)]/[1 - \alpha] + G^{[1]}(x, 0) \sum_{t=1}^{\infty} \alpha^{t-1} r_t(x), \end{aligned}$$

which is finite from (5.8) and (5.10). Therefore, $f_1(x), f_2(x), \ldots,$ is a bounded monotone sequence which implies (5.13). Monotone convergence implies that $f_1(\cdot), f_2(\cdot), \ldots,$ endow $f(\cdot)$ with their properties of concavity and monotonicity. ∎

The next result uses a familiar argument from inventory theory (Sobel 1970a) to prove that $f(\cdot)$ satisfies a functional equation analogous to (4.1). Let

$$J(x, y) = G(x, y) + \alpha E f(s[y, D]),$$

which exists by virtue of the following proof. The proof is much simpler than those of similar theorems in Brock and Mirman (1972) and Schechtman (1976).

THEOREM 5.3. *Assumptions* (3.1), (3.2), (3.4), (3.5), (3.7), (3.9), *and* (5.7)–(5.10) *imply*

$$\begin{aligned} f(x) &= \sup\{J(x, y) : y \in Y(x)\}, \qquad x \in X, \\ &= J(x, A[x]). \end{aligned} \tag{5.14}$$

Proof. For all x and n, $f_{n-1}(x) \leqslant f_n(x)$ so

$$J_{n-1}(x, y) \leqslant J_n(x, y) \leqslant f(x) \leqslant B(x) < \infty, \qquad y \in Y(x), \quad x \in X,$$

where $B(x)$ is the bound developed in the proof of (b) in Theorem 5.2. Therefore, $\{J_n(x, y)\}$ is a bounded monotone sequence so $J_n(x, y) \leqslant J(x, y)$ and

$$f_n(x) = \sup\{J_n(x, y) : y \in Y(x)\} \leqslant \sup\{J(x, y) : y \in Y(x)\}.$$

Convergence of f_n to f implies

$$f(x) \leqslant \sup\{J(x, y) : y \in Y(x)\}, \qquad x \in X,$$

so the theorem will have been proved after establishing

$$f(x) \geqslant \sup\{J(x, y): y \in Y(x)\}, \qquad x \in X. \tag{5.15}$$

Monotone convergence implies

$$f(x) \geqslant f_n(x) = \sup\{J_n(x, y): y \in Y(x)\},$$
$$f(x) \geqslant \lim_{n\to\infty} \sup\{J_n(x, y): y \in Y(x)\},$$

whereas the right side of (5.15) is

$$\sup\{\lim_{n\to\infty} J_n(x, y): y \in Y(x)\}.$$

Therefore, for (5.15) it is sufficient to prove

$$\lim_{n\to\infty} \sup\{J_n(x, y): y \in Y(x)\} = \sup\{\lim_{n\to\infty} J_n(x, y): y \in Y(x)\}. \tag{5.16}$$

The existence of the limit on the left side of (5.16) is implied by (5.13). For each n, $J_n(x, \cdot)$ is continuous on $Y(x) = [0, x]$ so $J_n(x, \cdot) \to J(x, \cdot)$ uniformly on $[0, x]$ because the Dominated Convergence Theorem implies $Ef_{n-1}(s[\cdot, D]) \to Ef(s[\cdot, D])$. Therefore,

$$0 = \lim_{n\to\infty} \sup\{J(x, y) - J_n(x, y): 0 \leqslant y \leqslant x\},$$

which implies (5.16) and, consequently, (5.15). ∎

$A(\cdot)$ inherits the properties of $\{A_n(\cdot)\}$.

Corollary 5.1. *The assumptions of Theorem* 5.2(a) *imply*

$$0 \leqslant A'(x) \leqslant 1. \tag{5.17}$$

6. ACCUMULATION USING A STATIONARY POLICY

Suppose the same policy $A(\cdot)$, arbitrary and possibly suboptimal, but satisfying (5.12), is used each period. Then reinvestment and consumption each period t are given by $A(\chi_t)$ and $\chi_t - A(\chi_t)$, where χ_t denotes the random asset level at the beginning of period t. Successive asset levels are connected by

$$\chi_{t+1} = s[A(\chi_t), D_t], \qquad t = 1, 2, \ldots, \tag{6.1}$$

or, equivalently, by a kernel $K(A(x), \Gamma)$ which is the probability of being in

$\Gamma \subseteq X$ if $A(x)$ is the action taken at state $x \in X$ (cf. Feller (1971)). More formally, consider the state space X with a Borel field of subsets B. Then $K(\cdot, \cdot)$ is a probability kernel if $K(x, \cdot)$ is a probability measure on B for each $x \in X$ and $K(\cdot, \Gamma)$ is a B-measurable function for each $\Gamma \in \beta$.

Whether or not the Markov processes χ_t converge to a stationary distribution is an important question. Convergence results in certain cases are given in Brock and Mirman (1972), Brock and Majumdar (1975), Mirman and Zilcha (1975), Schechtman (1976), and Schechtman and Escudero (1977). By comparison with these papers, the approach here relies on properties of the stochastic kernel $K(\cdot, \cdot)$. Therefore, the proofs are more direct and do not in any essential way depend on scalar properties of x_t and y_t (although the theorems are presented only for this case).

$K(\cdot, \cdot)$ induces the following operator T which takes bounded measurable functions h into bounded measurable functions:

$$(Th)(x) = \int K(x, dy)\, h(y). \tag{6.2}$$

There is a dual representation which takes probability measures Q into probability measures; namely, for each $\Gamma \subseteq X$,

$$(VT)(\Gamma) = \int Q(dx)\, K(x, \Gamma) \tag{6.3}$$

(Rosenblatt 1967). The operator T is equicontinuous if it maps continuous functions into continuous function. For the remainder of this section, suppose X is a compact set, $0 \in X$, and $s(\cdot, d)$ is continuous; note that (5.12) implies continuity of $A(\cdot)$. Therefore, it is straightforward to show that $K(\cdot, \cdot)$ induces an equicontinuous family of transformations. Consider the following three conditions:

(A) $K(x, I) > 0$ for all open intervals $I \subseteq X$.

(B) There exists a compact subset L of X, such that for each $x \in L$, $K(x, L) = 1$ and the operator T defined in (6.3) is irreducible on L in the sense of Rosenblatt (1967, p. 476).

(C) Neither (A) nor (B) holds.

Condition (A) is satisfied, for example, by models where $s(\cdot, \cdot)$ is linear, as in Schechtman and Escudero (1977), where $s(y, d) = ry + d$. Condition (B) is often proven as a preliminary result, as in Section 3 of Brock and Mirman (1972). Condition (C) is important when determining if a stationary distribution concentrates all its mass at a single point. The three conditions separate the question of the existence of a unique stationary distribution from the question of the existence of at least one, perhaps many, invariant measures on the set X, given some policy $A(x)$. Some of the literature confuses the two questions.

THEOREM 6.1. *If X is compact and $K(\cdot, \cdot)$ induces an equicontinuous family of transformatrions, then:*

(i) *There is at least one invariant measure on X.*

(ii) (A) *implies there is only one invariant measure on X and it is the unique positive stationary distribution on X.*

(iii) (B) *implies there is a unique invariant measure for each closed irreducible subset L of X, and this measure is the unique positive stationary distribution on L.*

(iv) *Suppose also, for some $\gamma > 0$, $P\{s(A[x], D) \geqslant x\} = 1$ for all $x \in [0, \gamma]$. Let $x^* = \sup\{x: x \in X\}$ and suppose $L = \{x: \gamma \leqslant x \leqslant x^*\}$ is irreducible. Then there is a unique stationary measure on X which has positive probability only on open intervals that intersect with L.*

(v) *If 0 is an absorbing state then* (C) *implies that there is a unique stationary distribution concentrated at 0 (so $P\{\liminf x_t = 0\} = 1$ and the process tends to gets arbitrarily close to 0).*

Proof. Part (ii) is Theorem 2 in Feller (1971, p. 272). Parts (i), (iii), (iv), and (v) are implied by Theorems 3 and 4 in Rosenblatt (1967) and Theorem 2.4 in Jamison (1964). ∎

Boylan (1977) proves theorems similar to (iv) and (v) although his approach is different. Two examples illustrate the power of the theorem. First, for the models in Schechtman (1976) and Schechtman and Escudero (1977), part (ii) of the theorem immediately implies convergence to a unique stationary distribution. Second, the model in Brock and Mirman (1972) has an equicontinuous kernel on a compact set so it necessarily possesses an invariant measure. This avoids the lengthy argument in Section 4 of Brock and Mirman's paper. Moreover, our results depend on irreducibility of an operator on a *subset* of the set of states so one can focus on states that "communicate" rather than on fixed points of growth functions. This permits simplified proofs of the results in Section 3 of Brock and Mirman's paper. Boylan (1977) gives such a simplified proof.

7. EXTENSIONS

The results thus far concern a model whose structure is stationary over time and in which growth does not occur. These restrictions can be relaxed.

Suppose, for example, that utility alters with age or time as well as with wealth. Let $G_k(x, y)$ denote the utility function appropriate to consumption at age $n-k$. Then all results in Section 4 and Theorem 5.1 remain valid if G is replaced by G_n in the assumptions in Section 3. As one example that generalizes Hakaanson (1973), let $G_k(\cdot, \cdot) \equiv 0$ if $k > 1$.

If the random variables $D_n, D_{n-1}, \ldots, D_2, D_1$ exhibit a dependence, let $T_k(D_n, \ldots, D_{n-k+1})$ denote a statistic of $D_n, \ldots, D_{n-k+1}$ that is sufficient for D_t. Let ϕ_k be a function which maps (T_k, D_{n-k}) into T_{k-1}. Such functions must exist, because the entire past history is a sufficient statistic. Then the results in Sections 4 and 5 through Theorem 5.1 remained unchanged if each $Y_n(x)$ is a convex set and $Y_n(x) \subseteq Y_n(x')$ if $x' \geqslant x$ for each n. If $Y_n(x)$ is appropriately convergent in n for each x, then generalization of Theorems 3.2, 5.3, and Corollary 5.1 can be obtained.

Exogenous price processes arise when there is a random sequence of prices $\rho_1, \rho_2, \rho_3, \ldots$, such that

$$G(x, y, \rho) = u(\rho[x-y])$$

and the constraint set is now $Y(x, p)$ for each fixed value p of ρ. If the assumptions in Section 3 are valid for each fixed value p of ρ, then the results in Sections 4 and 5 are true for each fixed p. For example, Theorem 5.1 becomes $f_{n-1}(x, p) \leqslant f_n(x, p)$, $A_{n-1}(x, p) \leqslant A_n(x, p)$, etc.

Undiscounted Utilities

The results in Section 4, Theorems 5.1 and 6.1 are true for all values of the discount factor $\alpha \geqslant 0$. If $\alpha \geqslant 1$ then generally $f_n(x) \to \infty$ as $n \to \infty$ so Theorems 5.2b and 5.3 are uninteresting. The validity of Theorem 5.2a is an intriguing issue when $\alpha = 1$.

The overtaking criterion (see Brock and Mirman (1973); Brock and Majumdar (1975) and their references to the work of Von Weizsacker, Gale, and Gale's students; Denardo and Rothblum (1979)) is currently in vogue when utilities are undiscounted. Consider, instead, the average gain criterion from the theory of Markov decision processes, namely,

$$\Gamma(Z \mid x) \equiv \varliminf_{T \to \infty} \sum_{j=1}^{T} G(x_j, y_j)/T \tag{7.2}$$

and search for a *gain-optimal* policy Z^* such that

$$\Gamma(Z^* \mid x) = \sup_Z \Gamma(Z \mid x) \qquad \text{for all} \quad x \in X.$$

It can be shown that a policy is gain optimal if it is overtaking optimal (using $\varliminf$ in the definition). The converse is generally false so gain optimality is a weaker criterion than overtaking optimality.

Blackwell (1962), Derman (1962), and subsequent writers have explored the connection between the discounted criterion as $\alpha \uparrow 1$ and the gain criterion. In order to apply Derman (1962) as in Sobel (1970b), suppose X is a finite set and $Y(x)$ is a finite set for each $x \in X$. Then C is a finite set so the set A_0 of mappings from X to Y (i.e., x is mapped into $Y(x)$ for each $x \in X$) is finite. Let A denote the finite subset of A_0 that comprises mappings satisfying (5.12). Thus A is finite too.

If $\alpha < 1$, Theorem 5.2(a) asserts the existence of an optimal policy that is a member of A. Let $A(x, \alpha)$ denote the dependence on $\alpha < 1$ of such a policy and let $\alpha_1, \alpha_2, \ldots$ satisfy $\alpha_k < 1$ for all k and $\alpha_k \to 1$. Then $A(\cdot, \alpha_k)$ is an element of A, a finite set, so the sequence $A(\cdot, \alpha_1)$, $A(\cdot, \alpha_2), \ldots$, must contain a subsequence all of whose members are the same element of A. Let $A(\cdot) \in A$ denote the policy corresponding to such a subsequence $\alpha_{n(1)}, \alpha_{n(2)}, \ldots$, i.e., $A(\cdot) \equiv A(\cdot, \alpha_{n(1)}) \equiv A(\cdot, \alpha_{n(2)}) \equiv \cdots$. Then the argument in Derman (1962) establishes

$$\Gamma(A(\cdot)|x) = \lim_{k \to \infty} (1 - \alpha_{n(k)}) f(x, \alpha_{n(k)}), \qquad x \in X,$$

$$\Gamma(A(\cdot)|x) = \sup_Z \Gamma(Z, x), \qquad x \in X,$$

where $f(x, \alpha)$ makes explicit the dependence of $f(\cdot)$ on the value of $\alpha < 1$. Therefore, $A(\cdot)$ is gain optimal. But $A(\cdot) \in A$ so $A(\cdot)$ satisfies (7.3).

Let $\mathbf{N}$ denote the set of natural numbers $\{0, 1, 2, \ldots\}$. Then the preceding argument justifies the following claim.

Theorem 7.1. *If* $X = \{0, 1, 2, \ldots, \sigma\}$ *for some* $\sigma \in \mathbf{N}$ and $Y(x) = \{[0, x] \cap \mathbf{N}\}$, $x \in X$ *then the assumptions of Theorem* (5.2a) *imply existence of a gain-optimal policy that satisfies* (5.12).

It would be interesting to verify Theorem 7.1 without restricting X and $Y(x)$ for each x to be finite sets. If only X is finite, then the problem still seems surprisingly delicate. Suppose in this case there exists

$$A(x) \equiv \lim_{\alpha \uparrow 1} A(x, \alpha), \qquad x \in X. \tag{7.4}$$

Results of Fox (1967) show that $A(\cdot)$ may *not* be gain optimal unless the Markov chain structure induced by $A(\cdot)$ is also the chain structure induced by every one of $A(\cdot, \alpha_k)$, $k = 1, 2, \ldots$, where $\alpha_k \uparrow 1$.

The difficulty of establishing (7.4) is another obstacle to generalizing Theorem 7.1. The difficulty does not seem to stem from finiteness of X. One might conjecture that optimal consumption is a nonincreasing function of α so that $A(x, \cdot)$ is nondecreasing for each $x \in X$. Then the limit in (7.4) would exist because $A(x, \alpha) \in Y(x)$ so $A(x, \alpha) \leqslant x$ from $Y(x) = [0, x]$ and $A(x, \cdot)$

would be a bounded monotone function. To establish monotonicity of $A(x, \cdot)$ one might exploit Theorem 5.2(a) and first establish monotonicity of $A_n(x, \cdot)$ for all n (let the dependence on α of $A_n(x)$ and $f_n(x)$ be explicit). A straightforward inductive proof shows for each n that $f_n(x, \alpha)$ is concave and nondecreasing as a function of α. However, this property does not ensure monotonicity for $A_n(x, \cdot)$. An argument similar to the proof of Theorem 4.2 shows that a sufficient condition would be $J_n^{(3)}(x, y, \alpha)$ nondecreasing in α (for each n, x, and y). In turn, $J_n^{(2)}(x, y, \cdot)$ would be nondecreasing if $f_{n-1}^{(1)}(x, \alpha)$ were a nondecreasing function of α (for each x). This last step has not been accomplished nor is there a counter example.

Bewley (1977) proves, essentially, that $A(x, \cdot)$ is nondecreasing for each $x \in X$ when $X = \mathbf{R}_+$, $Y(x) = [0, x]$, $s(y, d) \equiv y + d$, and $G(x, y) \equiv g(x - y)$ is differentiable and strictly concave. The steps of his proof are similar to those above which we had previously outlined.

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A PRELIMINARY REPORT ON BOTTOMFISHING IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Regional and day-night differences in the distribution and catchability of bottomfishes are shown through analysis of catch data collected by the National Marine Fisheries Service on cruises of the NOAA ship *Townsend Cromwell* in the Northwestern Hawaiian Islands. Large catches of opakapaka, *Pristipomoides filamentosus*, in the Nihoa to Gardner Pinnacles region are replaced by those of hapu'upu'u, *Epinephelus quernus*, further up the chain. Mean fish weight for several species increases going up the chain, possibly due to fishing pressure in the Nihoa to Gardner Pinnacles region. Day fishing results in a greater catch rate than night fishing. Preliminary growth estimates indicate that opakapaka takes 3.25 yr. and kahala, *Seriola dumerili*, takes 1.75 yr. to attain a 70-cm fork length.

bottomfish
age and growth
distribution and relative abundance

INTRODUCTION

With the creation of the 200-mile Fishery Conservation Zone in 1976 and the extensive fishing pressure around the main islands of Hawaii came the need for marine resource assessment of the Northwestern Hawaiian Islands (NWHI). Under the Tripartite Cooperative Agreement, the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service (NMFS) assumed responsibility for the quantitative fishery assessment and survey of benthic slope and pelagic resources of the NWHI (Uchida et al., 1979). One major portion of our responsibility is the deepwater bottomfish resource.

At present, the NWHI bottomfish resource supports a small commercial fishery which has been in existence since at least 1948. Due to the long distance between the NWHI and marketing ports, most of the commercial fishing effort has been limited to the area between Nihoa and Gardner Pinnacles.

The Insular Resource Task of NMFS has examined various aspects of biological and fishery data on the NWHI demersal fishery. Studies on the feeding habits (see paper by Humphreys), spawning and fecundity (see paper by Kikkawa), occurrence of ciguatoxin (see paper by Ito and Uchida), and age and growth (J.H. Uchiyama, Southwest Fisheries Center Honolulu Laboratory, NMFS, NOAA, Honolulu, Hawaii 96812, personal communication, March 1980), are in various stages of completion. This report will discuss the distribution and relative abundance of the demersal fishes obtained from our survey cruises and the progress on age and growth studies on opakapaka, *Pristipomoides filamentosus*, and kahala, *Seriola dumerili*.

MATERIAL AND METHODS

The sole source of information used in this paper is the catch data obtained by NMFS on cruises of the *Townsend Cromwell* from October 1975 to May 1979. During this period, the *Cromwell* occupied 112 handline fishing stations on eight cruises in the NWHI. Except where otherwise stated, all references to catch refer to the catch of the eight most important commercial species caught by the *Cromwell*: opakapaka; ehu, *Etelis marshi*; onaga, *E. carbunculus*; kalekale, *P. sieboldii*; gindai, *P. zonatus*; butaguchi, *Caranx cheilio*; kahala; and hapu'upu'u, *Epinephelus quernus*.

Fishing operations were conducted while drifting near the edge of the banks at bottom depths varying from 30 to 200 fathoms. Our handline gear consisted of lines with from 2 to 15 hooks (Nos. 20 to 30) per line. We generally used hydraulic or electric gurdies to aid in line retrieval and occasionally fished manually retrieved lines as well. The most commonly used bait was stripped squid. In processing the catch, we recorded species, sex, weight, and both standard and fork or total length measurements. Where appropriate, we preserved gonads, stomachs, tissue samples, and otoliths for future analysis at the laboratory.

On the *Cromwell* we usually retrieve lines as soon as one fish is on, regardless of the number of hooks we are using. For this reason, I chose line-hours rather than hook-hours as an estimate of fishing effort. In data analysis, I used catch per unit effort (CPUE) by station both for weight (kilogram) and numbers of each species as two measures of relative abundance and catchability.

I used analysis of variance (ANOVA) to test the null hypothesis that location in the chain, species, and day-night factors have no effect on CPUE. Since there were insufficient data to allow for a bank-by-bank analysis, I divided the project area into three regions. Region I, Nihoa through Gardner Pinnacles, represents the area fished by commercial vessels on a regular basis. Region II, Raita Bank through Lisianski Island, is separated from Region III, Pearl and Hermes Reef through Kure Atoll, by a natural break in the chain. In the test for day and night differences in catchability, the separations between day and night stations were not distinct, so I arbitrarily placed data into day or night categories depending on whether most of the fishing effort occurred before or after 0600 and 1930 hours.

We followed the methods of Struhsaker and Uchiyama (1976) in cleaning, mounting, and reading otoliths for age determinations.

RESULTS

The CPUE of the combined catch of all commercial species varied considerably among stations. Many stations had no catch at all whereas at one Midway Island station, the catch rate was 43.3 kg/line-hour (9.3 fish/line-hour). On a bank-to-bank basis, overall catch rates ranged from 0 at Salmon Bank and an unnamed bank northeast of Midway to 12.6 kg/line-hour (3.1 fish/line-hour) at Pearl and Hermes Reef. A portion of this variation may be due to the wide range in fishing effort at the various stations and banks (0.5 to 32.3 line-hours and 3.3 to 231.7 line-hours, respectively). Regional catch data for each species are presented in Table 1 for day, night, and overall catches. Table 2 compares day and night CPUE by weight for each species. Catch composition of the five major species in numbers by region is displayed in Figure 1 (onaga, gindai, and kalekale make up such a small portion of our catch that they are not included in this figure). Table 3 lists the incidental species caught with their overall catch rates.

In a three-way ANOVA of CPUE in terms of weight, significant differences in CPUE were found among regional ($P = 0.02$), species ($P = < 0.01$), and day-night ($P = 0.01$) classifications and with region to species ($P < 0.01$) and species to day-night ($P = 0.02$) interactions. In a three-way ANOVA with CPUE in terms of numbers, however, significant differences were found in only three cases: species, day-night, and region to species. In a one-way ANOVA of mean fish weight by region for each species, significant differences were found for ehu between Regions I and II, and I and III; hapu'upu'u between Regions I and II; kahala between Regions I and III; and gindai between Regions I and II. Results of a chi-square test of the number of fish caught by species by region show significant differences in species composition by region.

We have collected otoliths from fish of all of the commercially important species mentioned in this paper. Preliminary growth curves for opakapaka (Figure 2) and kahala (Figure 3) have been estimated from otolith examinations (Uchiyama, personal communication, March 1980). Laboratory, NMFS, NOAA, Honolulu, Hawaii 96812, personal communication, March 1980).

TABLE 1. COMMERCIAL CATCH DATA FOR BOTTOMFISH IN THE NORTHWESTERN HAWAIIAN ISLANDS

Species	Region I				Region II				Region III			
	Catch		CPUE		Catch		CPUE		Catch		CPUE	
	No.	Weight (kg)	No.	Weight (kg)	No.	Weight (kg)	No.	Weight (kg)	No.	Weight (kg)	No.	Weight (kg)
All species												
Day	589	2,028.6	1.815	6.251	321	1,506.2	1.785	8.377	178	769.2	1.841	7.954
Night	219	707.2	1.117	3.608	72	369.2	0.769	3.944	113	456.0	1.447	5.839
Total	808	2,735.8	1.552	5.256	393	1,875.4	1.437	6.860	291	1,225.2	1.665	7.009
Ehu												
Day	99	132.2	0.305	0.407	90	195.8	0.501	1.089	67	136.8	0.693	1.415
Night	62	105.7	0.316	0.539	21	42.8	0.224	0.457	30	46.1	0.384	0.590
Total	161	237.9	0.309	0.457	111	238.6	0.406	0.873	97	182.9	0.555	1.041
Opakapaka												
Day	245	817.3	0.755	2.519	40	163.4	0.222	0.909	0	0	0	0
Night	89	255.0	0.454	1.301	4	15.8	0.043	0.169	7	34.3	0.090	0.439
Total	334	1,072.3	0.642	2.060	44	179.2	0.161	0.655	7	34.3	0.040	0.196
Hapu'upu'u												
Day	75	424.9	0.231	1.309	79	562.2	0.439	3.127	57	338.4	0.589	3.499
Night	17	114.1	0.087	0.582	22	147.0	0.235	1.571	47	203.2	0.602	2.602
Total	92	539.0	0.177	1.036	101	709.2	0.369	2.594	104	541.6	0.595	3.098
Butaguchi												
Day	66	409.1	0.203	1.261	55	297.4	0.306	1.654	32	162.7	0.331	1.683
Night	7	24.5	0.036	0.125	8	37.1	0.085	0.396	7	35.8	0.090	0.458
Total	73	433.6	0.140	0.833	63	334.5	0.230	1.223	39	198.5	0.223	1.136
Kahala												
Day	36	173.6	0.111	0.535	30	232.3	0.167	1.292	8	96.8	0.083	1.001
Night	22	183.0	0.112	0.934	11	114.4	0.118	1.222	15	117.2	0.192	1.501
Total	58	356.6	0.111	0.685	41	346.7	0.150	1.268	23	214.0	0.132	1.224
Gindai												
Day	25	35.3	0.077	0.109	22	36.3	0.122	0.202	0	0	0	0
Night	5	8.6	0.026	0.044	5	11.0	0.053	0.117	0	0	0	0
Total	30	43.9	0.058	0.084	27	47.3	0.099	0.173	0	0	0	0
Kalekale												
Day	42	28.5	0.129	0.088	2	1.2	0.011	0.007	8	3.8	0.083	0.039
Night	16	9.8	0.082	0.050	1	1.1	0.011	0.012	5	3.7	0.064	0.047
Total	58	38.3	0.111	0.074	3	2.3	0.011	0.008	13	7.5	0.074	0.043
Onaga												
Day	0	0	0	0	3	15.8	0.017	0.088	6	30.7	0.062	0.317
Night	1	6.6	0.005	0.034	0	0	0	0	2	15.6	0.026	0.200
Total	1	6.6	0.002	0.013	3	15.8	0.011	0.058	8	46.3	0.046	0.265

TABLE 2. OVERALL CATCH PER UNIT EFFORT FOR DAY AND NIGHT FISHING STATIONS

Species	CPUE (weight)		Ratio
	Day	Night	
Ehu	0.77	0.53	1.45
Opakapaka	1.63	0.53	1.96
Hapu'upu'u	2.21	1.26	1.75
Butaguchi	1.45	0.26	5.58
Kahala	0.84	1.13	0.74
Gindai	0.12	0.05	2.40
Kalekale	0.06	0.04	1.50
Onaga	0.08	0.06	1.33
All species together	7.16	4.17	1.72

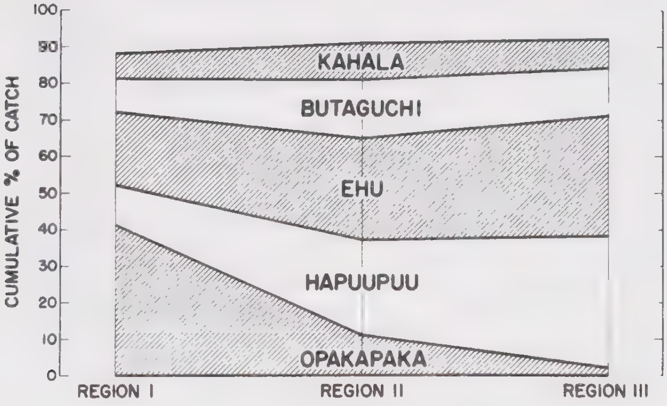

Figure 1. Catch composition by region in terms of numbers

TABLE 3. CATCH OF INCIDENTAL SPECIES IN THE NORTHWESTERN HAWAIIAN ISLANDS

Species	Catch		CPUE	
	Number	Weight (kg)	Number	Weight (kg)
Gempylidae				
Promethichthys prometheus	47	20.6	0.049	0.021
Carangidae				
Caranx lugubris	13	41.0	0.013	0.042
C. ignobilis	38	349.7	0.039	0.361
C. speciosus	1	0.9	0.001	0.001
C. sexfasciatus	1	0.7	0.001	0.001
C. melampygus	3	11.6	0.003	0.012
Carangoides ferdau	3	18.1	0.003	0.019
Elagatis bipinnulatus	2	20.2	0.002	0.021
Priacanthidae				
Priacanthus sp.	5	2.7	0.005	0.003
Holocentridae				
Myripristis sp.	6	2.0	0.006	0.002
Tetraodontidae (*Sphoeroides cutaneus* and *Lagocephalus* sp. included)	17	9.1	0.018	0.009
Scorpaenidae				
Pontius macrocephalus	9	10.7	0.009	0.011
Scorpaenopsis cacopsis	1	1.5	0.001	0.002
Scorpaena colorata	1	0.7	0.001	0.001
Labridae				
Bodianus bilunulatus	5	5.7	0.005	0.006
B. oxycephalus	7	14.1	0.007	0.015
Lutjanidae				
Aprion virescens	1	7.5	0.001	0.008
Pristipomoides auricilla	2	1.6	0.002	0.002
Scombridae				
Scomber japonicus	3	5.2	0.003	0.005
Sarda orientalis	3	13.3	0.003	0.014
Mullidae				
Mulloidichthys pflugeri	1	1.4	0.001	0.001
Parupeneus porphyreus	1	1.4	0.001	0.001
Sphyraenidae				
Sphyraena sp.	4	4.0	0.004	0.004
Synodontidae				
Trachinocephalus myops	1	0.6	0.001	0.001
Muraenidae				
Gymnothorax berndti	1	0.9	0.001	0.001
Squalidae	2	7.3	0.002	0.008
Carcharhinidae	8	--	0.008	--

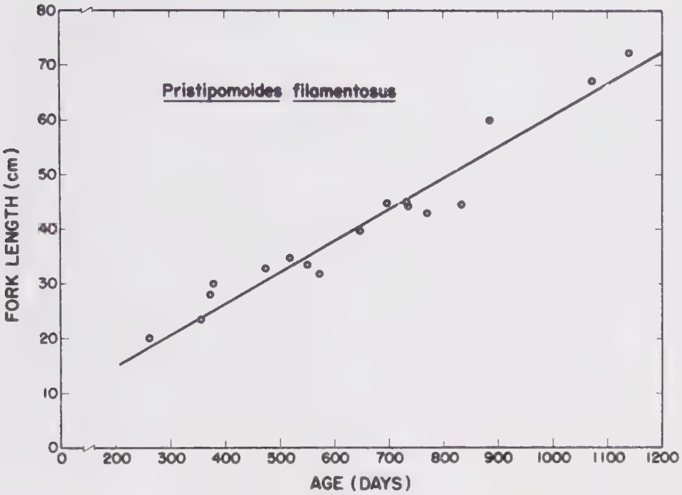

Figure 2. Preliminary growth curve for opakapaka, *Pristipomoides filamentosus*

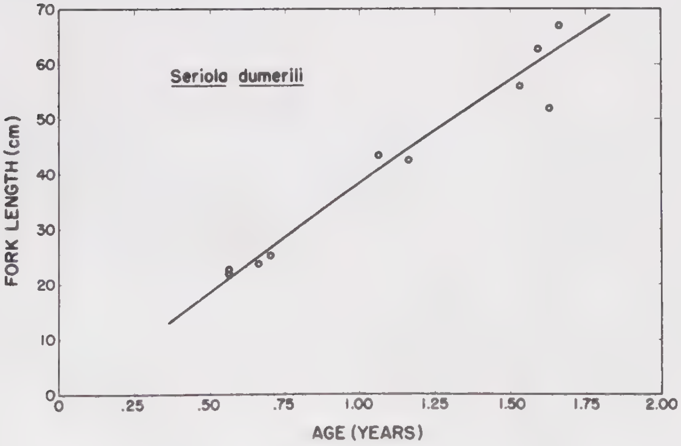

Figure 3. Preliminary growth curve for kahala, *Seriola dumerili*

DISCUSSION AND CONCLUSIONS

The three-way ANOVA tests showed that the regional increase in overall CPUE in terms of weight for the combination of all commercial species presented in Table 1 is significant ($P = 0.02$) whereas the change in CPUE in terms of number is not ($P = 0.12$). This results in an increase, by region, in the mean weight of the hypothetical composite commercial bottomfish. There are two possible explanations for this increase. Either the mean weight of individuals within a species is increasing or a generally larger species comprises a greater percentage of the catch on a regional basis from Regions I to III. To check on the first possibility, I ran a one-way analysis of variance of mean fish weight by region for each species. As mentioned in the results section, ehu, kahala, gindai, and hapu'upu'u showed significant regional differences in mean weight. Also, in all significant cases, mean weight increased between Regions I and II or I and III. Thus, increase in mean weight of fish by species does contribute to the overall increase in CPUE by region. This may be an indication of fishing pressure in Region I where mean weights were significantly lower for these species, or it may be due to other factors such as temperature or habitat differences between regions.

The significant difference in CPUE in terms of numbers by species by region shown in the three-way ANOVA indicates that there is a change in species composition by region, as well. Cell values for variance in the chi-square test showed that opakapaka and hapu'upu'u are major contributors in this difference. These changes in relative abundance for opakapaka and hapu'upu'u are shown graphically in the species composition by region (Figure 1). The difference in overall mean weights for opakapaka (4.0 kg) and hapu'upu'u (6.8 kg) indicates that the regional change in the species composition is also a factor in the regional increase in CPUE in terms of weight.

Day and night differences in catchability are also significant. Results of the three-way ANOVA show that day and night CPUE in terms of weight is significantly different on both an overall and by-species basis. Differences in day and night CPUE are presented in Table 2 as the ratio of day CPUE to night CPUE. As can be seen, the day CPUE is, in general, higher than the night CPUE. In fact, the only commercial species with a higher CPUE at night is kahala. The day-night difference is particularly noticeable for butaguchi where the day CPUE is over five times greater than the night CPUE. These differences in catchability may be due to changes in feeding activity between day and night or a nightly migration away from the areas that we normally fish. Similar trends were found for CPUE in terms of number, but they were not found to be significant on a species basis.

Commercially, fishing for opakapaka is usually conducted at night with night catches reported to be far better than day catches (C. Yamamoto, captain, FV *Koko*, Honolulu, Hawaii 96814, personal communication, May 1980 and W. Shinsato, captain, FV *Taihei Maru*, Honolulu, Hawaii 96814, personal communication, May 1980). That our results differ from the experiences of commercial fishermen is probably due to the differences in fishing techniques employed. On the *Townsend Cromwell* we fish close to the bottom while drifting for both day and night fishing operations. Commercial fishermen on the other hand, may drift fish during the day, but at night they usually anchor over opakapaka grounds, chum to aggregate the fish, and fish well off the bottom (up to 15 fathoms).

Our studies of age and growth of bottomfishes are still in the preliminary stages. We have made age estimates on a few specimens of each of the commercial species discussed in this paper. We still have many otoliths to read, but we do have enough data to establish tentative growth curves for opakapaka (Figure 2) and kahala (Figure 3). Because we have no data for fish outside of the size ranges of those used to generate the curves, estimates of age using these curves should be limited to fish falling within these ranges. For greater confidence in our growth estimates, we must verify the temporal nature of the suspected daily growth increments on otoliths. We are currently conducting experiments to mark otoliths by tetracycline injections in captive fish (e.g., opakapaka; akule, *Trachurops crumenophthalmus*; papio, *Caranx* sp.; and malu, *Parupeneus pleurostigma*) to verify the temporal periodicity of otolith growth increments.

FUTURE RESEARCH NEEDS

Much work remains to be done in this project. At the conclusion of the field work, we should have enough catch information to make a bank-by-bank analysis of distribution and relative abundance of bottomfishes in the NWHI. We should also have enough otoliths read to determine reliable growth curves for all the commercial species. Reliability of these curves, of course, will be largely dependent upon verification of the daily nature of the otolith growth increments. This, combined with future progress in other areas under current investigation (fecundity, spawning season, foraging habits, and ciguatoxin), will give us a fair understanding of the biology and catchability of bottomfishes in the NWHI.

There are other areas of investigation that would also be helpful. Recording the time of day that each fish is caught, rather than just the duration of the station as we presently do, would give a much better picture of the catchability of each species throughout the day. It is possible that there are some interesting relationships, such as increased catchability at dawn and dusk, that are obscured by present methods of data collection.

Fishing operations should be conducted while at anchor using chum to aggregate fish. This technique should produce high catches. Catch results using this technique could then be compared with those obtained while drift fishing.

A study of recruitment has been proposed by NMFS which is designed to exert heavy fishing pressure on a small bank followed by monitoring the recovery of fish stocks. Results from this study would produce a better estimate of bottomfish stocks in the NWHI than is now available.

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Examination of Layered Tissues of Odontocetes for Age Determination Using Polarized Light Microscopy

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ABSTRACT

The polarized light microscope with a 1/4 λ plate greatly improves resolution of the microstructure in layered hard tissues of dolphins by revealing changes in crystallographic alignment not visible using more conventional instruments. In adult specimens of *Stenella attenuata* the prenatal enamel contains up to 240 striae that are thought to represent daily records of prenatal growth. Prenatal dentine contains approximately 60 incremental layers, the significance of which is unknown at present. In *Lagenorhynchus, Delphinus, Tursiops* and *Stenella* spp. the neonatal 'line' consists of several incremental layers, suggesting that post-parturitional trauma may be a prolonged event. In these species the postnatal dentine contains 13 regularly-spaced accessory layers in the first five or six growth layer groups (GLGs). These accessory layers are thought to reflect lunar cycles, and each contains an average of 28 microlayers (lines of von Ebner) that may represent daily growth increments. Cemental GLGs show fewer accessory layers than those of dentine. GLGs in periosteal bone consist of accessory layers that may reflect lunar cyclicity. It is suspected that layering in dentinal, cemental, and periosteal tissues is in response to the same cyclic influences.

INTRODUCTION

Investigators of dolphin life histories routinely use compound or dissecting microscopes to identify and count growth layer groups (GLGs) in thin sections of teeth and bones to determine relative ages. These instruments operate with plain light that is either transmitted through a section or reflected from the surface of a section to detect differential optical densities or topographic relief delineating GLG boundaries thought to represent uniform segments of time.

A prime cause of disagreement among investigators in counting layers has been the difficulty in deciding where to separate the layers. Also, there may be difficulty in distinguishing any regular layering at all in sections that have not undergone special preparation. The polarizing microscope assists in overcoming some of these problems by expressing structural and histological differences as highly contrasted patterns of light (i.e. as different colors or shades). It accentuates structure, not visible using more conventional instruments, that is of potential importance in studies of dental development, and it provides further bases for understanding and interpreting layering patterns for age determination.

This paper is an account of preliminary research conducted using the polarizing microscope in examination of the layered structure of hard tissues of dolphins as an aid to understanding more fully the macrostructures useful in estimating ages.

BACKGROUND

The petrographic polarizing microscope was developed initially to determine the mineral composition of rocks by examination of their crystallography. It is a compound microscope with light-polarizing and phase-contrast capabilities that can be used to define differential optical and crystallographic features of translucent objects prepared in thin section (Moorehouse, 1959). The technique has been used widely in comparative dental histological studies (e.g. von Keil and von Nolting, 1968; Peyer, 1968).

Dental and periosteal tissues of dolphins and other vertebrates contain the mineral hydroxyapatite. Because growth is inconstant, layers of various optical densities are formed, and crystal lattices of hydroxyapatite are deposited within the layers in orientations that tend to differ from increment to increment but which have a common alignment within a given growth increment. When layered tissue is examined with polarized light, each crystallographic alignment, and variations in the composition of the mineral phase and organic matrix are made visible.

MATERIALS AND METHODS

1. Ontogenetic series

Teeth and samples of periosteal bone, from the 'pan' region of the mandible and from the premaxillae at the base of the rostrum, were collected from approximately 50 female specimens of *Stenella attenuata* from the eastern tropical Pacific–the animals ranged from early fetal to old adult. Materials were prepared in undecalcified thin section (≅ 250 μm) and arranged in order of body length to form developmental series. Each series was examined under polarized light in an effort to characterize developmental stages in the layering patterns and to inter-calibrate dentinal, cemental, and periosteal growth-layer-group (GLG) patterns.

2. Known-age specimens

Thin sections (≅ 250 μm) of undecalcified teeth from captive-born (known-age) individuals of *Tursiops truncatus* were examined by polarized light microscopy, without my advance knowledge of their ages, in an effort to identify reliable structures that may be useful in determining absolute ages.

3. Tetracycline-marked specimens

Several teeth from specimens of *Tursiops truncatus, Lagenorhynchus obliquidens,* and *Delphinus delphis* containing tetracycline-marked tissues were examined by polarized light and under ultraviolet reflected light to intercalibrate postnatal dentinal and cemental layers. One of the known-age specimens was incidentally marked with tetracycline while *in utero*. The marked tissue was examined to identify the structural time of birth.

4. Preparation of samples

All teeth were sectioned mid-longitudinally using a *Buehler Isomet* saw equipped with two diamond-embedded blades separated by a 200-μm shim to produce a wafer 200 μm to 300 μm thick. Bone samples were sectioned transversely using the same equipment. Thin sections were mounted on glass slides with *Permount* and covered with glass coverslips.

5. Method of examination

All sections were examined at between 57 x and 1200 x using a *Zeiss* photomicroscope No. 472190 equipped with a rotatable polarizer and analyzer, a rotary stage, petrographic objectives, and a 1/4 λ (first order red) quartz plate. A fluorescent vertical illuminator with a filter-reflector No. 44-77-05 combination was used for examination of the tetracycline-marked specimens in ultraviolet light.

RESULTS AND DISCUSSION

1. Enamel

A. ***Ontogenetic development of layers.*** Enamel is deposited prenatally. Polarized light microscopy of this tissue in *Stenella attenuata* reveals up to 240 growth lamellae lying parallel to each other, arranged in an offlapping pattern downward from near the apex and oriented subnormal to the prismatic structure (Fig. 1). Analyses of the ontogenetic series indicate that these layers represent growth increments that first appear in teeth of fetuses at body lengths of between 25 cm and 28 cm. There is an increase in the number of layers with increasing body length. At 50 cm the enamel contains approximately 40 layers, at 70 cm there are 150 layers, and in teeth of full-term fetuses (approximately 82.5 cm) and postnatal animals including old adults (up to 220 cm) up to 240 enamel layers have been counted. This suggests that incremental growth in enamel probably does not continue after parturition.

B. ***Significance and possible applications of enamel layering.*** Perrin, Coe and Zweifel (1976) concluded that the average gestation period for *S. attenuata* is approximately 11.5 months (or 345 days). If the layers in the enamel represent daily growth, as much as 240 days (or 8 months) of fetal development could be accounted for. The unrecorded 3.5 months would represent the period from conception to the stage at which the tooth germ is developed immediately prior to layer formation.

If examination of larger samples substantiate these tentative findings, enamel layers may be used in conjunction with labelling of fetal hard-tissues in captive, pregnant females and with embryological data from terrestrial mammals to estimate more precisely the fetal growth stages and gestation periods of delphinid species.

2. Prenatal dentine

A. ***Ontogenetic development of layers.*** Prenatal dentine has been relatively ignored except as a 'landmark' tissue internal to which GLG counts are begun. It has been described as unlayered or granular in appearance, but polarized-light

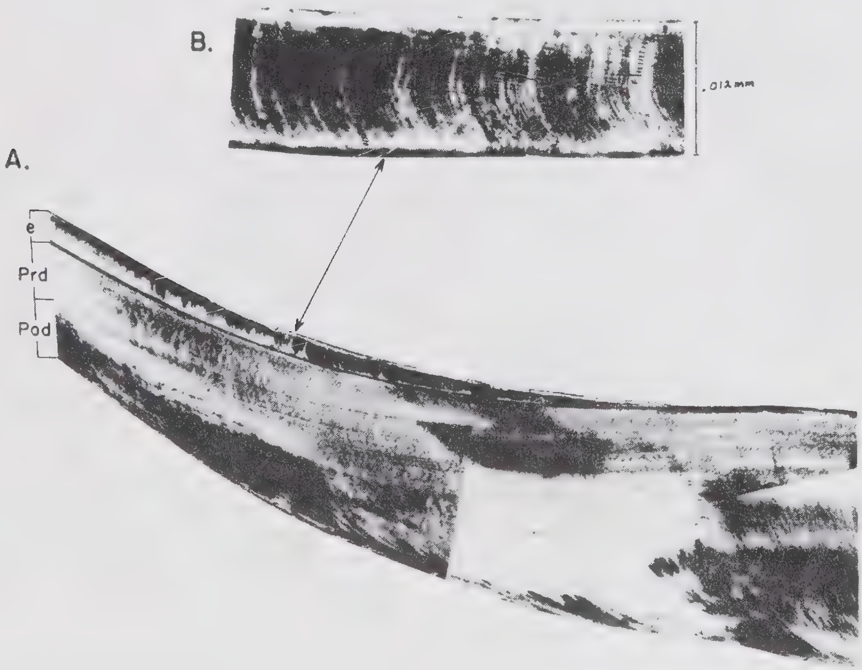

Fig. 1. Daily (?) layering in enamel in a tooth of a female of *Stenella attenuata* (TCF 060).
A. Half of a tooth section viewed with polarized light and showing layering in the enamel (arrow) (57x).
B. Highly magnified section of enamel as shown in A showing layers as indicated by marks. Because of the oblique (offlapping) arrangements of layers many transects at various intervals from apex to neck may be necessary to obtain full counts. A total of 223 enamel layers was seen in the tooth.
Abbreviations: e. enamel, n. neonatal line, prd. prenatal dentine, pod. postnatal dentine.

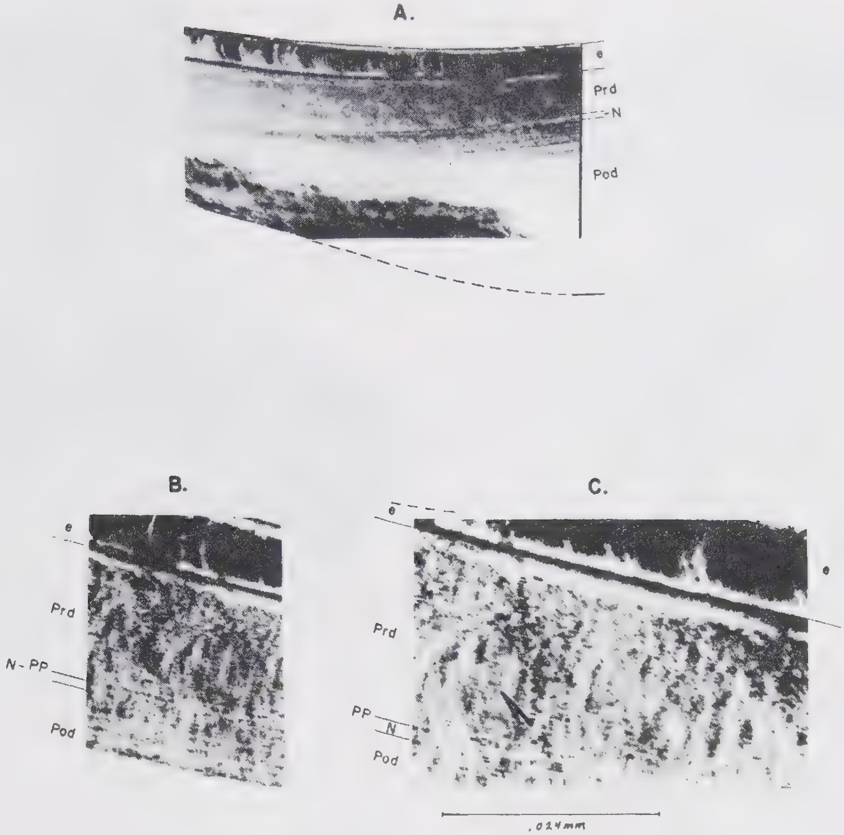

Fig. 2. Layering in prenatal dentine and neonatal line in *Stenella attenuata* (TCF 060).
A. Thin section of half of tooth as viewed with crossed polarizers and phase contrasted light showing prenatal dentine and neonatal line with layers not readily apparent (57x).
B. Magnified view (200x) of prenatal dentine as in A showing layering in prenatal dentine and neonatal line.
C. Highly magnified view (250x) of same section as in B with 60 counted layers in the prenatal dentine and 5 layers visible in the neonatal layer. Major layers often bifurcate in prenatal dentine (arrows). Note that layering is difficult to resolve in the earliest deposited tissue near the enamel. Abbreviations: PP. structural point of parturition, N neonatal line.

microscopy reveals that layers are fairly well developed in prenatal dentine (Fig. 2).

Layers first appear at the same stage of fetal development as do layers in enamel, i.e. at 25 cm to 28 cm. Unlike enamel layering however, prenatal layers seem to accumulate at a considerably lower rate. At 50-cm body lengths the teeth show only 25 prenatal dentinal layers, at 70 cm approximately 45 layers are present, and in the teeth of full-term fetuses and postnatal animals only 55 to 60 layers have been counted.

B. ***Significance of prenatal dentinal layering.*** The significance of layering in this tissue is not readily apparent. If prenatal dentinal growth occurs concomitantly with that of enamel (i.e. for a presumed period of approximately 240 days), then prenatal dentinal layers would be deposited at an average rate of one every four days. Such a rate would not seem to be correlated to any known exogenous cycle. On the other hand, distinguishing layers in this tissue is difficult, especially in the region of earliest deposition (Figs. 2B–C). It is possible that either some of the 'growth pulses' governing layering in enamel are not of sufficient intensity to produce visible layers in the prenatal dentine, or that another technique is needed to detect existing, but indistinct layers.

3. Neonatal line

The neonatal 'line' has been thought to demarcate the point of parturition–recording post parturitional trauma of the neonate as it is confronted with the external environment and a new mode of feeding. Polarized-light microscopy at 200 × shows that this 'line' is composed of an alternating series of three or more pairs of opaque and translucent layers bounded on either side by a rather bright translucent layer (Figs. 2B–C).

4. Postnatal dentine

A. *Composition of GLGs.* Microscopic examination (at 57 ×) of postnatal dentine using plain transmitted or reflected light reveals repeating or semi-repeating patterns

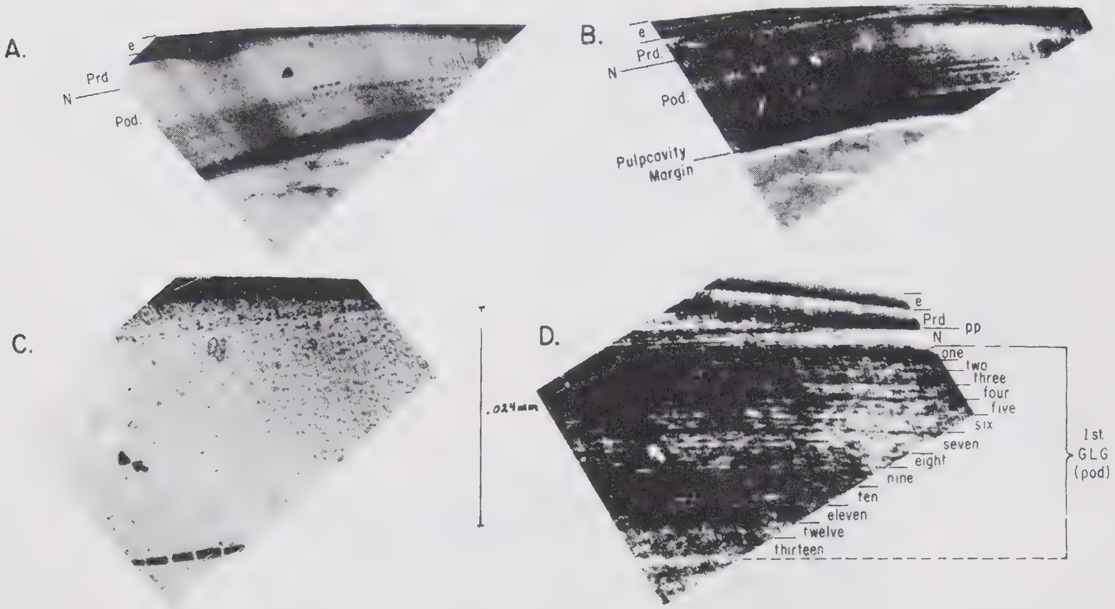

Fig. 3. Lunar layering in postnatal GLGs of a tooth of a specimen of *Stenella attenuata*.
A. Plain-light view of one-half of tooth section showing postnatal dentine. Dashed line indicates boundary between first and second growth layer groups. Triangle (an artifact) used as point of reference (57x).
B. Section as in A, viewed with crossed polarizers and phase-contrasted light. Note presence of multiple layers brought out by this technique.
C. Plain-light view of section as in Fig. A (250x). Arrow indicates triangle reference point.
D. Section as in C viewed with crossed polarizers and phase-contrasted light. Note layered components of neonatal line and 13 counted accessory layers within first GLG (bracketed). At this power the more intense aggregations of microlayers (lines of von Ebner) become apparent. Abbreviation: GLG = growth layer groups.

of accessory layers that may be used to define GLGs. Each accessory layer consists of a pair of components—a translucent layer and an opaque layer, which, in turn, are composed of fine dark and light incremental layers. With ordinary light microscopy, accessory layers are seen to occur in varying intensities, and commonly the accessory layers that mark the boundaries of GLGs are no more distinct than some of the more strongly developed accessory layers within the GLGs. Hence problems often arise in defining GLGs that introduce considerable subjective error into age estimates.

Polarized light microscopy of the tissue enhances resolution of accessory layers already optically apparent using more conventional microscopes and makes visible other accessory layers that cannot otherwise be detected easily. At 200 X the first (i.e. externalmost) GLG is shown to consist of 13 accessory layers excluding the one represented by the neonatal layer (Figs. 3D and 4). Although younger GLGs are deposited as increasingly thinner, more compressed layering sequences, the first three or four GLGs usually show 13 accessory layers also (Figs. 3 and 4). Younger GLGs usually are too thin to permit delineation of all incremental components, but in large, well layered teeth 13 accessory layers can be detected in the fifth and (rarely) sixth GLGs.

B. ***Possible significance of accessory layers.*** There are 13 lunar months (synodic cycles) in a year. It is possible that, as in many other marine organisms, the physiologies of odontocetes are or were influenced either directly or indirectly by lunar periodicity and that this periodicity is reflected in the layering patterns of hard tissues. If accessory layers correspond with lunar cyclicity, they could be used as countable units to determine age. To test this, accessory layers in the teeth of two known-age specimens of *Tursiops truncatus* ('Pinger' and 'Moe B') were counted without advance knowledge of their true ages. Teeth of both specimens contained between 42 and 45 accessory layers. 'Pinger' (SWFC 0007) was born in captivity at the Naval Ocean Systems Center, San Diego in November 1970 and died in February 1974 (Hui, 1978). 'Moe B' (SWFC 0008) was born at Sea World in San Diego on 14 April 1975 and died on 4 July 1978. Both animals were 3 years, 3 months old (or 43 lunar months old). The close agreement between the number of accessory layers counted and the age of the specimens in lunar months strengthens the hypothesis that accessory layers, when optimally viewed, may be used to estimate ages for young specimens.

C. ***Lines of von Ebner: daily(?) records.*** At high magnifications (800 to 1200 X), polarized-light microscopy of postnatal dentine reveals a system of minute incremental growth layers (so-called 'lines of von Ebner') within the accessory layers (Figs. 3D and 5). Often these structures are difficult to see, but in accessory layers where they are most distinctive, I have counted an average of 28 such microlayers. Because they are contained within accessory layers that I interpret to represent 28-day lunar cycles, I suggest that the lines of von Ebner in dolphin teeth may reflect daily growth.

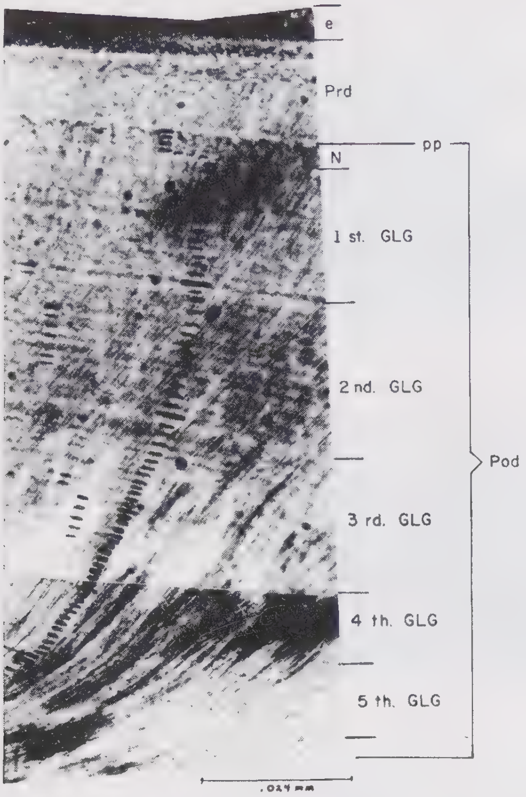

Fig. 4. Partial tooth section of a female specimen of *Stenella attenuata* (TCF 060) viewed with cross polarizers and phase-contrasted light. Section shows 13 regularly spaced accessory layers in each of the first five GLGs (each GLG defined by translucent boundary layers) (200x). Regular spacing and number of accessory layers indicated lunar cyclicity (see text).

5. Cementum

A. *Resolution of GLGs.* In the teeth of most species of small delphinids, cemental GLGs are difficult to define without special preparations because of the extreme thinness and poor layering of this tissue. Typically, cementocytes are stratified, but their parallel alignments do not correspond necessarily to cemental layering where it is distinguishable.

Compared to ordinary light, polarized-light microscopic examination provides somewhat better resolution of cemental layers because of the color contrast produced. Nevertheless, only decalcification and staining procedures (Kasuya, 1977) seem to enhance cemental layering adequately.

B. *Accessory layers.* When visible under polarized light, GLGs in cement exhibit fewer accessory layers than the 13 found in early dentinal GLGs. Tooth sections of captive specimens of *T. truncatus* clinically treated with tetracycline show fluorescent markers in the dental tissue when examined microscopically with reflected ultraviolet light (Figs. 6A, B, C and D). These markers extend down the dentinal layers, wrap around the bases of the teeth, and are continuous with markers within the cemental tissue (Figs. 6C and D). This indicates that the same mechanism which governs dentinal layering also influences cemental layering, but it is not known why fewer accessory layers are found in the cemental GLGs. The problem may be one of preparation and examination techniques (see Kasuya, 1977).

6. Periosteal bone

Polarized-light microscopy helps in delineating GLGs in transverse sections of periosteal bone from the 'pan' region of the mandible (Fig. 7) and from the premaxilla near the base of the rostrum (Fig. 8). A small ontogenetic series of bone samples compared with teeth from the same individuals indicates that periosteal GLGs seem to accumulate at the same rate as dentinal GLGs. In old specimens, some resorption of the early periosteal GLGs takes place, but relicts of these resorbed layers remain discernible with the polarizing microscope (Fig. 8).

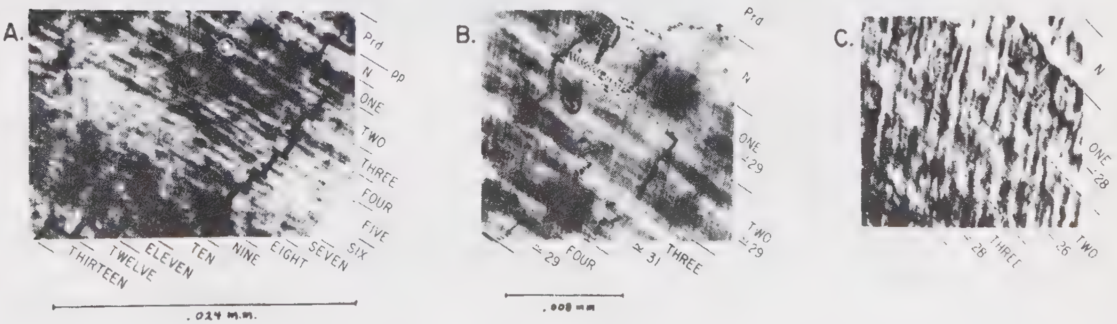

Fig. 5. Daily layering in postnatal GLGs in *Stenella attenuata.*

A. Magnified view (250x) of layers as shown in Fig. 3D showing 13 (bracketed) lunar layers within the first growth layer group.

B. Magnified view (800x) of inset in 5A, showing system of lines of von Ebner in first four accessory layers. Counts average 29 lines per accessory layer. This suggests that daily growth is represented. Circled arrow points to small triangle in second accessory layer used as point of reference.

C. Lines of von Ebner in another region of same tooth showing greater resolution produced by changing angle of section relative to polarizers. An average of 27 or 28 lines may be seen in first three accessory layers (800x).

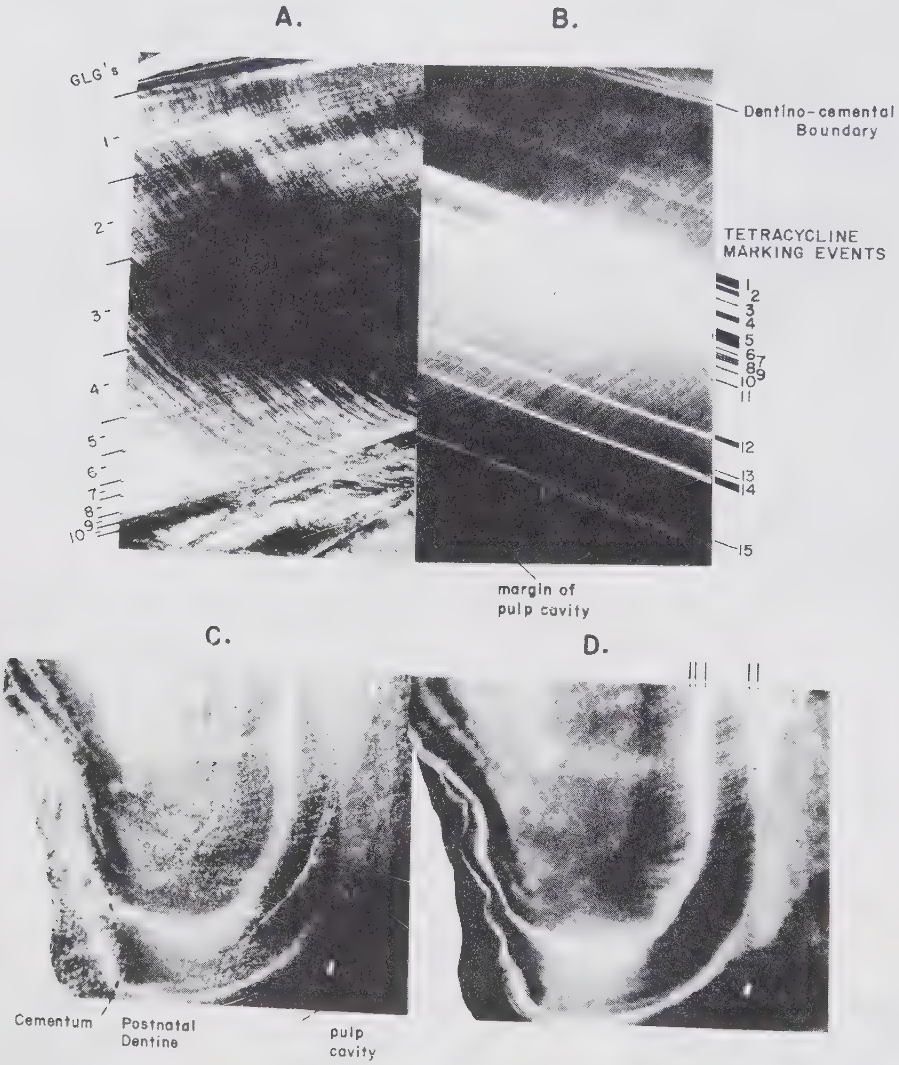
A.
B.
GLG's
1
2
3
4
5
6
7
8
9
10
Dentino-cemental Boundary
TETRACYCLINE MARKING EVENTS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
margin of pulp cavity
C.
D.
Cementum
Postnatal Dentine
pulp cavity

Fig. 6. Tetracycline-marked partial tooth sections of *Tursiops truncatus* (#AB718) showing fluorescent bands in relation to layers in postnatal dentine and cementum.

A. Dentinal tissue viewed using polarized light, showing GLGs.

B. Mirrored view of dentinal tissue as shown in A viewed under ultraviolet light showing flourescent bands (150x).

C. Base of tooth viewed using combination of reflected ultraviolet light and transmitted plain light showing relationship of fluorescent markers to layers in cementum and dentine (150x).

D. Base of tooth viewed under ultraviolet light showing continuity of flourescent markers in dentine and cementum (150x).

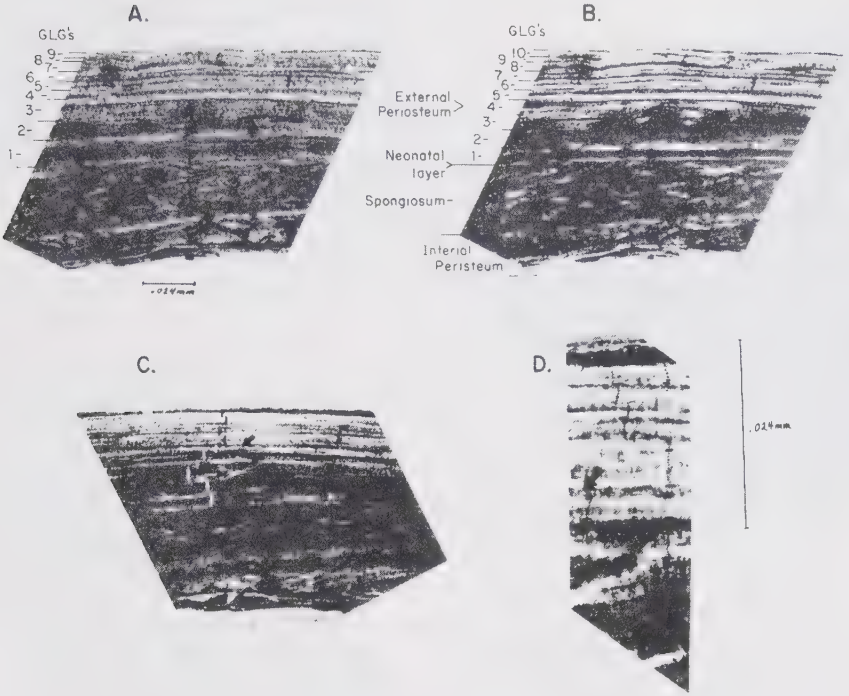

Fig. 7. Periosteal layering in mandible of *Stenella attenuata* female (TCF 060).
A. Transverse section of mandible from the "pan" region viewed in plain light (57x).
B. Section as in A showing strong contrast between GLGs produced by polarized and phase-contrasted light.
C. Another section of same bone viewed with polarized light. GLGs are marked. Arrow indicates point of reference between fifth and sixth GLG (57x).
D. Magnified (150x) area of section as in C showing 13 accessory layers per GLG.

The technique shows also that each periosteal GLG is composed of 13 accessory layers–most apparent in early layers (Fig. 7D). As in the dentinal GLGs the accessory layers within later GLGs in the bone become compressed. The presence of lunar-cycle layers in bone suggests that dentinal, cemental, and periosteal layering is influenced by a common mechanism. If this proves to be true, eventually all three layering systems may be used interchangeably to obtain maximum age estimates of very old individuals in which dentinal layering has stopped because of pulp-cavity occlusion.

SUMMARY

Polarized-light microscopy gives high resolution and color contrast to the ultrastructure in layered hard tissues of delphinids. Visual access to the ultrastructure is useful in gaining a more complete understanding of the factors influencing layering and layering rates. With the use of this method to examine ontogenetic series (in *S. attenuata*), and known-age and marked tissues of other delphinids – the following tentative conclusions were reached:

(1) Enamel layers occur that may represent daily growth records. Because enamel is developed prenatally, the layers may be used in concert with other reproductive and embryological data to estimate gestation periods and fetal age-growth stages in dolphins.

(2) The neonatal line is a complex layer, the initial component of which may mark the point of parturition. The presence of its other components may indicate that post-parturitional trauma is a prolonged event.

(3) The prenatal dentine has a layered pattern that commences consonantally with enamel layering, but its layering rate may be governed by different physiological factors.

(4) Each of the first five or six postnatal dentinal and periosteal GLGs are composed of 13 accessory layers that seem to correspond to lunar months. If this is true, the age of young animals may be estimated more accurately than in the past.

(5) Lines of von Ebner in postnatal dentine of delphinids may represent daily growth.

(6) Cemental, dentinal, and periosteal layering probably is influenced by the same physiological mechanism. This may eventually permit use of all three systems interchangeably in estimating ages of old animals.

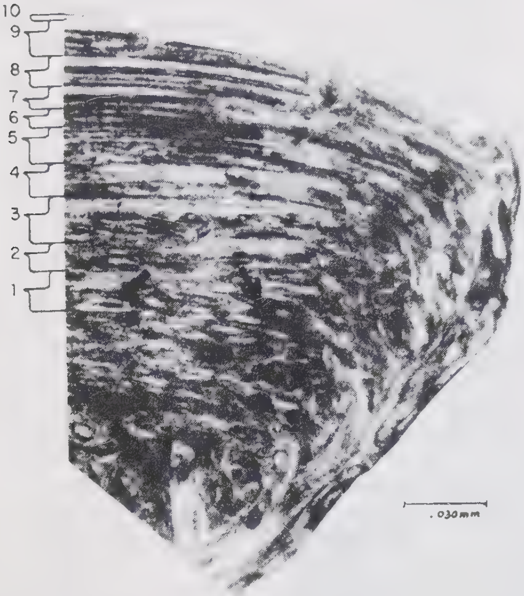

Fig. 8. Periosteal layering in premaxilla of *Stenella attenuata* female (TCF 060).

A. Transverse section of premaxillary bone taken near base of rostrum and viewed with polarized light, showing GLGs. The first GLG shows incipient resorption as indicated by presence of secondary Haversian systems (arrows) (80x).

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Some Approaches to Calibration of Age in Odontocetes Using Layered Hard Tissues

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ABSTRACT

Current methods in determining age of odontocetes rely upon untested assumptions. The relationship between layering and absolute age requires calibration. To achieve this goal, five approaches are suggested:

(1) the establishment of a reference collection for known-age, minimum known-age, and time-marked samples;
(2) the construction of developmental series of layered hard tissues representing individuals from various taxonomic and geographical stocks;
(3) the tagging and recovery of wild animals that have been time-marked;
(4) an extended program of multiple time-marking and extraction of teeth of live-captive animals; and
(5) the study of layered hard tissues in conjunction with clinical records of specimens treated with fluorescent antibiotics.

Pilot programs using these approaches are in various stages of implementation at the Southwest Fisheries Center, La Jolla.

INTRODUCTION

Recent studies of odontocete life histories have used counts of layers in teeth and in bones to estimate individual ages preparatory to constructing age-composition and growth models of dolphin populations. The models rely on the sweeping assumption that layers are deposited in hard tissues of odontocetes yearly in a manner analogous to the process of tree-ring formation.

Specifically, the working assumptions seem to be, first, that layering occurs at approximately constant rates; second, that yearly layers may be defined by convenient breaks that occur between dark and light zones in the tissue; and third, that the dark-light components of putative annual layers reflect physiological responses to seasonal change or to some other regular fluctuation in the external environment. Despite the 'soft' data used in interpreting layers in terms of age, it is also assumed that the results are sufficiently accurate for constructing meaningful life history models for various species of odontocetes.

Our present knowledge of the factors contributing to hard-tissue layering in odontocetes is insufficient to justify the use of the above assumptions as though they are proven hypotheses. The general physiology of cetaceans is poorly understood, and it is not known what causes layering in the hard parts of dolphins. Despite years of study, there exists little direct evidence that layering occurs at a constant or predictable rate, although it is true that a progressive increase in layers stands as some measure of increasing age. The few published studies that have used small samples of known-age teeth (Hui, 1978; Sergeant, Caldwell and Caldwell, 1973) or of single treatments to time-mark specimens (Best, 1976; Gurevich, Stewart and Cornell, this volume), have demonstrated only that the known elapsed time may be divided into a pattern of layers (i.e. that layers may be interpreted in such a manner as to obtain the age that is already known for the specimen). Results of a recent exercise reported by Kimura (this volume), involving experienced readers who counted dentinal layers of known-age specimens, underscore the problem that when the age is unknown, counts of number of layers are subjective and variable.

Although experience in defining growth layer groups (GLGs, terminology of workshop report, this volume) in teeth of specimens of known age is an important first step in the right direction toward calibration, such exercises are by no means a panacea for the problem of obtaining accurate age estimates. Nor should they seriously be regarded as more than a poor alternative to direct monitoring of layering rates in living animals. The exercises do not provide adequate support for inferring either that accumulation rates are constant, or, that 'annual' layers composed of dark and light subunits represent yearly records. Pulp-cavity occlusion, tooth wear, and poorly defined layering in dentinal, cemental, and periosteal tissues, as well as subjective interpretations of results using non-standardized techniques, may impair accurate reconstructions of life histories of even the most well known species.

This paper suggests various approaches that may be used to test the assumptions discussed above.

APPROACHES

Calibration of layered structure with absolute age (if indeed such is feasible) must be regarded as a goal of first priority and critical to accurate models of odontocete population dynamics. The appropriate tools are available for assessing the feasibility of real-time calibration, and opportunities now exist for applying these tools. The following approaches are suggested for assessment.

(1) The use of small numbers of specimens for which the layering period is known prevents confident conclusions about layering rates, but retrospective calibrations of large samples of such specimens could add measurably to this block of circumstantial evidence. A considerable amount of material exists from time-marked, e.g. tetracycline-injected, known-age (captive-born), and known minimum-age (wild-captured and held in captivity) animals representing a number of odontocete species, but at present it is held by a large number of individuals and institutions, some of whom do not fully realise its potential value in age/layer calibrations.

An international center (or centers) should be established as a permanent repository for all available time-marked, known-age, and known minimum-age specimens. The designated center would be charged with the responsibility of collecting and maintaining such specimens as a systematic reference library for use by all specialists engaged in age determination of odontocetes.

(2) A primary problem in calibration is the difficulty in defining countable units in layered tissue. Because hard-tissue layering patterns are complex and variable, it is important to understand to what extent differences in age, sex, and geographical stock influence such variability.

As available, teeth and samples of bone should be collected and prepared in thin section to construct ontogenetic series demonstrating developmental sequences of layer accumulation in individuals taken from discrete geographical and taxonomic stocks. The ontogenetic series would be ordered according to body length and sexual maturity and separated by sex. They should be curated centrally and be made available for study upon request.

(3) The possibility exists that layering rates and patterns among wild animals are different from those among animals maintained in captivity.

As economically and technologically feasible, experiments should be carried out to tag wild odontocetes *en masse* and time-mark their hard tissues by tetracycline injection. Eventual recovery of some animals through stranding salvage, incidental kill associated with commercial fisheries, or through other means would provide information on layering rates and patterns.

(4) Captive animals exist in numbers sufficient for comparative studies of layering rates and of factors that may influence layering in odontocetes.

Long-term studies should be carried out to time-mark and to periodically extract teeth of odontocetes maintained in captivity in order to monitor layering. Ideally, the experiments should be performed on reasonably large samples of dolphins representing both sexes and various age groups and should include controlled feeding exercises that would permit investigators to examine the possible effects changes in diet or in feeding frequency may have on layering. Experiments might be designed to alter water temperature, water salinity, or day length. Such experiments should require continuous observational records of any apparent changes in behavior, physiology, or proximate environment that may later be correlated with layering events. Eventually, results of experiments conducted near equatorial zones might be compared with results of experiments carried out on the same species in more temperate areas to examine the possibility that seasonality may alter layering patterns or rates.

(5) Many animals maintained in research and commercial oceanaria are treated routinely with medicines containing antibiotics, such as tetracycline, which combine with the hard tissues. When thin sections of layered tissue from these animals are examined microscopically under ultraviolet light, the markers fluoresce. By identifying the dates of the treatments, especially if the treatments were multiple, it is possible to calibrate the layered tissue with these fluorescent time envelopes, and thus, to calculate layering rates.

Veterinary records of marine mammals from commercial and scientific aquaria should be researched to identify preserved specimens that may have been incidentally time-marked, during medical treatment, with fluorescent or otherwise detectable drugs. If incidental marks are found to be multiple and incorporated into dentinal, cemental and periosteal layering systems, it may be possible to intercalibrate layers of all three systems with real time, allowing any system to be used alternatively. This would be valuable in cases of older specimens where dentinal deposition has ceased because of pulp cavity occlusion or where early periosteal bony layers have been resorbed.

PILOT PROGRAMS

Pilot programs with the above goals in mind are in various stages of implementation at the Southwest Fisheries Center in La Jolla.

(1) A literature search is underway to collect references to experiments or studies of known-age and time-marked specimens, or of captive animals for which time in captivity has been documented. Samples or specimen loans are being requested from individuals and institutions who are in charge of such specimens in order that we may prepare, examine and photograph them. Specimens that have been sequestered through donation will be organized into a permanent systematic collection. Photos and pertinent data for specimens in the collection and on loan to us will be maintained in a data file and eventually will be computerized. Requests for specimen donations or loans will be made also to acquaria and other institutions likely to have known-age or time-marked specimens in their charge.

(2) Sections of teeth and bone selected from early fetal through adult animals are being processed to construct comprehensive developmental series of males and females for *Tursiops truncatus, Delphinus delphis, Stenella attenuata* and *Stenella longirostris.* As adequate samples are accumulated, documented and catalogued, they will become available for study upon request.

(3) As part of school composition and cohesion experiments carried out on wild dolphins in the eastern tropical Pacific by NMFS scientists aboard the M/V *Queen Mary* chartered for dolphin/tuna research by the U.S. Tuna Foundation in September-October 1978, 331 offshore spotted dolphins, *S. attenuata,* were captured, measured, sexed, tagged, tetracycline-marked, and returned to the wild. Because this species is associated with the yellowfin tuna fishery, operations of which are being monitored by NMFS scientific technicians aboard many purse seiners, there is a good chance that at least some tagged specimens will be returned. Returns should enable us to compare hard tissue accumulation rates in wild dolphins with those in captive dolphins.

(4) A three-year project is being implemented, in cooperation with Hubbs/Sea World Research Institute, to monitor layering rates using tetracycline injections and tooth extraction. The study is using a large sample of healthy captive delphinids. In addition to developing data on layering rates, the study will attempt to identify such factors as age, sex, diet, handling and treatment, seasonal fluctuations in water temperature, and intergeneric vari-

ability, that may influence or alter layering patterns. The project will use a minimum of 12 specimens of *Tursiops truncatus,* representing approximately equal numbers of males and females and including animals of various relative ages. Animals of other species will also be used to develop data on delphinids in general.

Teeth will be prepared and examined under ultraviolet light to locate fluorescent marks, which will be used to calibrate growth layer groups in stained and unstained specimens.

(5) When microscopically examined under reflected ultraviolet light, thin-sectioned teeth from several captive specimens have revealed multiple fluorescent marks within their dentinal layers. Efforts are being made to obtain veterinary data for these specimens in an attempt to identify treatment dates, dosages, and the kinds of antibiotics used to treat these animals. In the absence of these data, I have identified growth layer groups to estimate the real time represented as bracketed by the fluorescent markers. This was done as a test of the assumption that growth layers are accumulated at a constant rate. Veterinary data, when obtained, will be used to test the estimates of time intervals represented between the markers.

CONCLUSION

The approaches and pilot programs outlined above offer means by which the long standing assumptions in age determination from layered tissues may be tested extensively. The progress made along these lines will depend upon the cooperation of members of the scientific community and of other persons in charge of animals, preserved skeletal materials, and medical records from commercial aquaria. Only through such cooperative efforts may we expect to address the many other difficult questions of dolphin life histories with some assurance.

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PERCENTAGE OF STARVING NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE SEA AS ESTIMATED BY HISTOLOGICAL METHODS

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ABSTRACT

The proportion of starving larvae of northern anchovy, *Engraulis mordax*, was estimated for the Southern California Bight in March 1977 from histological examination of larvae for 64 1 m net tow samples. The number of larvae in the tows varied from 0 to about 400. Approximately 6 per tow were sectioned and examined with the light microscope. Twenty-six specimens were identified as emaciated from anomalies of the trunk musculature and digestive tract. Some of the emaciated larvae occurred as isolated cases at widely scattered locations, but most were from a few nearshore tows, indicating "patches" of starving larvae. Temperature and plankton volume data indicate that the patches were associated with fluctuating environmental conditions. The samples indicate that about 8% of northern anchovy larvae in the Southern California Bight were starving.

One of the goals in investigations of pelagic fish stocks is that of predicting how large year classes will be at the time they are recruited to the fishery. One of the primary approaches to this problem has been the estimation of larval mortality rates based on abundance estimates from egg and larval surveys. While such surveys will probably continue to be the most reliable source of information on abundance at early ages, the high costs and time delays in processing samples are reasons for seeking alternative approaches (Hunter 1976b). Recently, Lasker (1975, in press) has developed a promising index based on availability of food in concentrations suitable for survival of early feeding stages of the northern anchovy, *Engraulis mordax*.

This study reports another approach that could provide an independent prediction of year class strength for the northern anchovy; namely, estimation by histological methods of the proportion of larvae in the sea showing symptoms of starvation. Since level of mortality in a population is likely to be some function of the proportion of larvae observed to be starving, the proportion, if based on adequate sampling, could be an indicator of ultimate year class success.

Condition factor (Blaxter 1971), chemical indices (Ehrlich 1974), morphometric analyses (Shelbourne 1957; Nakai et al. 1969; Ehrlich et al. 1976; Theilacker 1978), and histological analyses (Umeda and Ochiai 1975; O'Connell 1976; Theilacker 1978) have all been used with some success to characterize the starving condition in larvae of various marine species, in most cases under controlled laboratory conditions. The histological approach differs from the others in that the criteria of starvation are based on qualitative changes in the character of cells and tissues, not on quantitative measurements. Histological criteria developed earlier for northern anchovy larvae starved in the laboratory (O'Connell 1976) were the principal guidelines for evaluating the condition of ocean-caught larvae in this study.

METHODS

In March 1977, 64 net tows were taken over a 12-d period from the NOAA ship *David Starr Jordan* to obtain northern anchovy larvae for histological study. Almost half of the tows were taken between 2 and 10 mi (3.7-18.5 km) from the coast, most were near Newport Beach, Calif., where northern anchovy eggs and larvae were abundant, but some were much farther offshore. A surface temperature was taken by bucket thermometer at each net tow station.

Net tows were taken with a 1 m plankton net on which the cod end was a cylindrical Plexiglas[2]

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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bucket (length 30.5 cm, diameter 10 cm) that could be removed quickly. Tows were of short duration to minimize the time larvae would be under stress during capture. The net was let out at a fast steady rate to a depth of 20 m, and then retrieved at a moderate rate. The mean tow time was 3 min (SD = 40 s).

The net drained rapidly as it was hauled out of the water, leaving the cod end cylinder filled with water containing a light to moderate amount of plankton. The contents of the cylinder were immediately poured into a small sieve made of 0.505 Nitex mesh netting, and the sieve was then suspended in Bouin's fluid to fix the concentrated plankton. The total elapsed time from start of tow, when the plankton net first entered the sea surface, to submergence in Bouin's averaged 5 min, 8 s (SD = 1 min, 9 s). After the initial fixation, about 10 or 15 min, the sample was transferred from the sieve to a jar of fresh Bouin's, and this was replaced by 70% ethyl alcohol 2 or 3 d later.

In carrying out the above procedure the inside of the plankton net was not washed down after retrieval until the cod end containing the sample had been removed. After the cod end was removed, the inside of the net was hosed down thoroughly in preparation for the next tow.

Subsequent to the cruise, all northern anchovy and other fish larvae were sorted out of the samples and counted. From those tows containing only a few northern anchovy larvae, all were set aside for sectioning. From those tows containing many larvae, about half a dozen were chosen for sectioning. The number was approximately doubled for a few samples of special interest, e.g., offshore banks. Specimens were picked at random by putting all northern anchovy larvae from a given tow in a shallow, wide-mouth container and repeatedly dipping with a vial as the contents were swirling slowly. During this procedure small specimens with obvious yolk sacs were rejected because they represented nonfeeding larvae not yet vulnerable to starvation.

The total number of larvae selected for sectioning was 318. Standard length was measured with an ocular micrometer, then each specimen was imbedded in paraffin, sectioned serially as close to the sagittal plane as feasible, and stained in Harris' hematoxylin and eosin-phloxine B. Prior to microscope examination the mounted specimens were put in random order with their identities concealed.

Histological criteria similar to those diagnostic for laboratory starved larvae were readily established for ocean-caught larvae by preliminary examination of a few dozen (unidentified) specimens, after which all ocean-caught larvae were classified as to condition. Under Results, the histological indications of condition are described first, and then the classification of larvae is examined in relation to other variables, i.e., standard length, geographical distribution, temperature, and plankton volume.

RESULTS

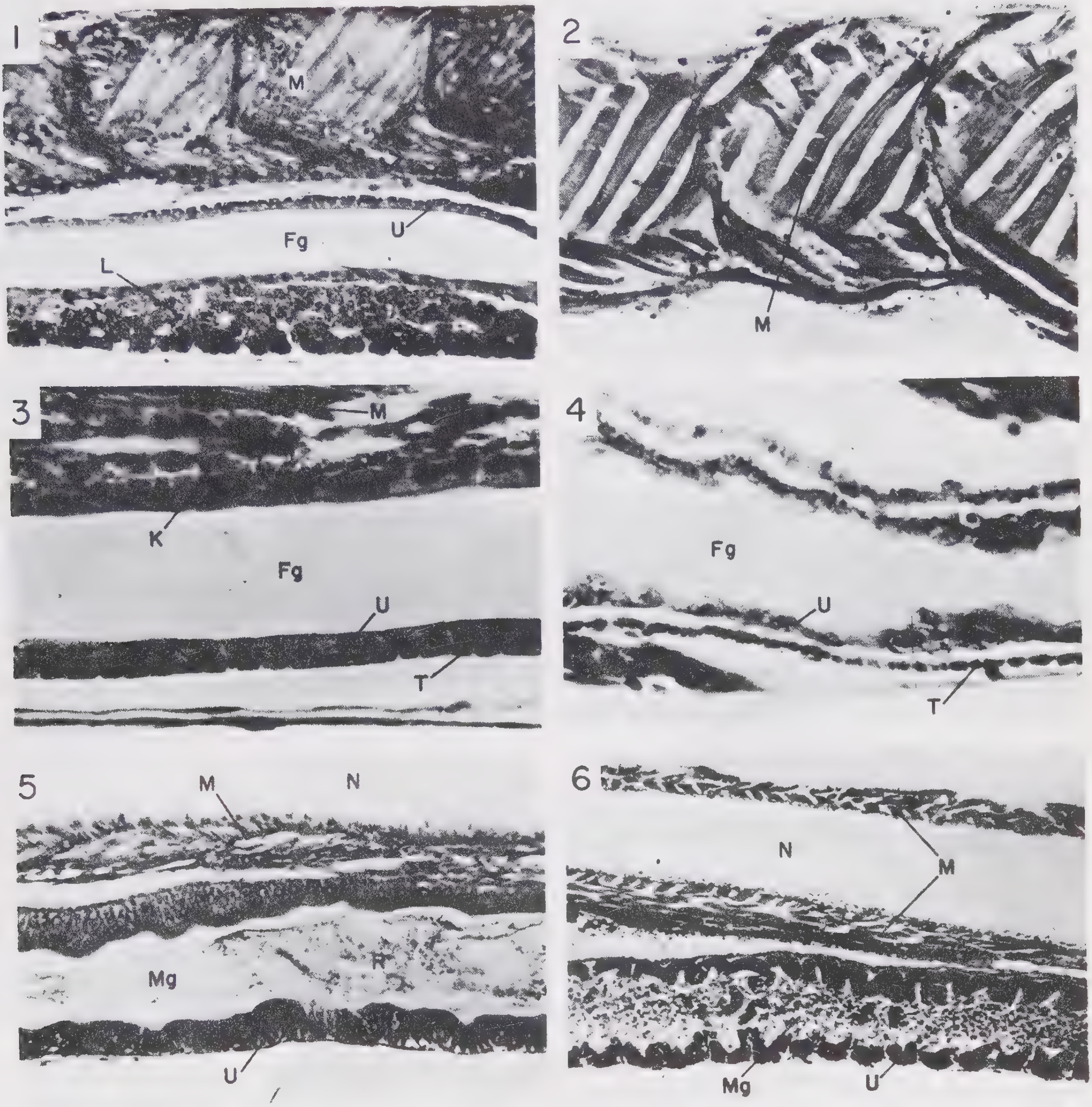
Histological Characteristics of Condition

O'Connell (1976) found the most noticeable effects of artificial starvation of northern anchovy larvae just beyond yolk absorption (3-5 mm) to be cellular dissociation with loss of zymogen in the pancreas, separation and hyalinization of trunk muscle fibers, and shrinkage of the notochord. In the ocean-caught material examined in the present study, specimens ranging from 2.5 to 10 mm showed anomalies in the trunk musculature and notochord, and occasionally also in the pancreas, that closely resembled the effects of starvation in the laboratory material. These larvae almost always showed, in addition, certain irregularities in the histology of the foregut and the midgut that were more striking than effects seen in the digestive tracts of artificially starved larvae.

Trunk Musculature

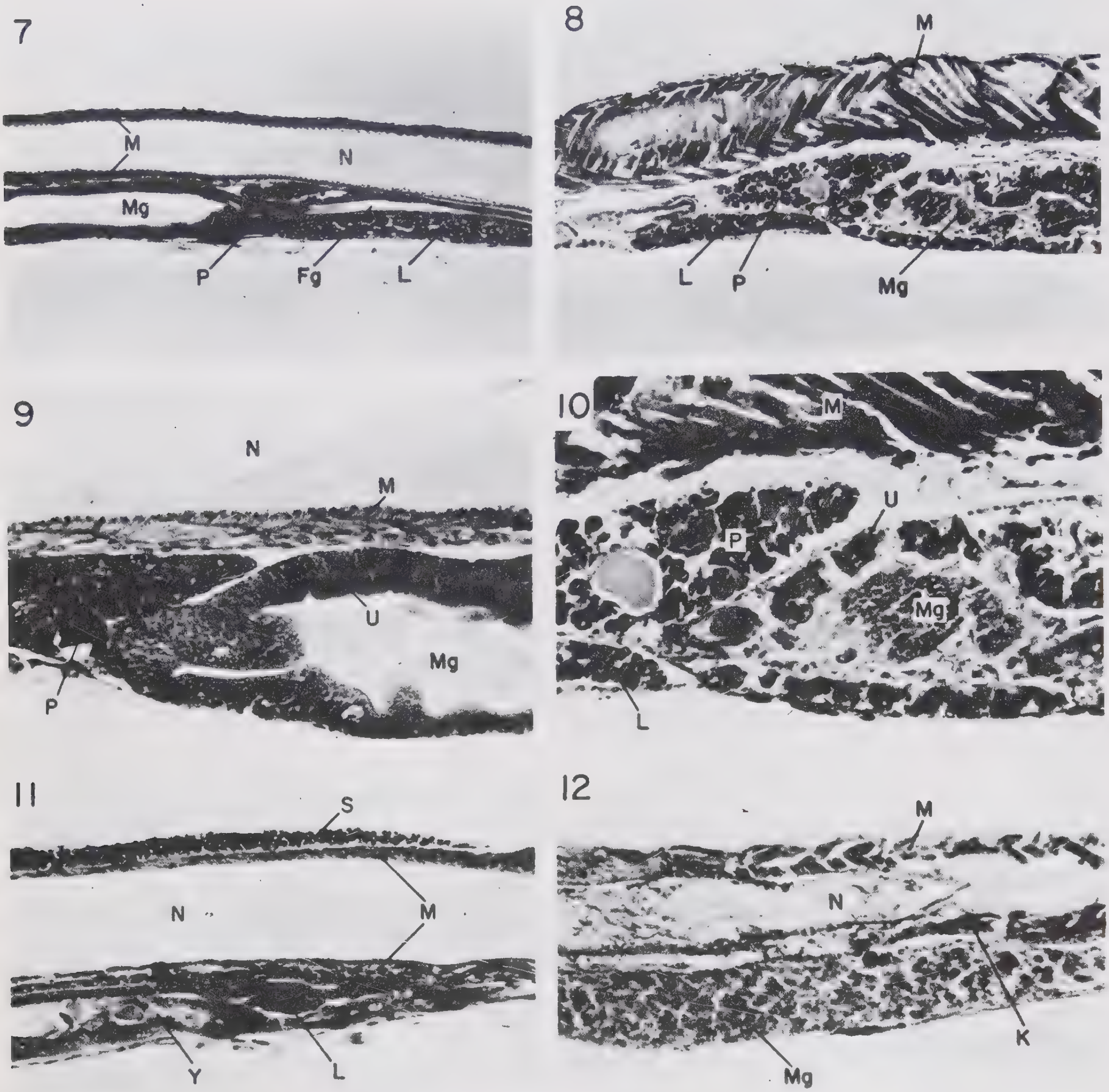
The trunk musculature in the majority of larvae showed good integrity and texture, forming a compact, solid sheet over the lateral surfaces of the notochord, with evident intermuscular matrix tissue and only occasional small separations (Figure 1). The notochord in such larvae generally had a smooth profile and was rarely separated from the musculature. In some specimens, however, the muscle fibers were noticeably separated from each other throughout, indicating an anomalous condition. In the more extreme cases (Figure 2) the fibers were widely separated with degraded fibril clarity, and matrix tissue was greatly reduced. In such specimens the notochord was also irregular in profile, imparting a "lumpy" shape to the trunk of the animal as a whole.

Degraded musculature, of course, might be the result of some process other than starvation. One possibility is capture myopathy, which has been



FIGURES 1-6.—Histological comparisons of healthy (left) and emaciated (right) northern anchovy larvae. All sections are approximately sagittal. 1) The trunk musculature, cut tangential to the body surface, forms a solid sheet. The foregut mucosa is composed of uniform cuboidal cells. 6.1 mm SL; 250×. 2) The trunk musculature, cut tangentially, shows widely separated fibers. 8.5 mm SL; 250×. 3)The foregut mucosa is composed of uniform thick cuboidal cells. 7.0 mm SL; 630×. 4) The foregut is irregular and the cells of the mucosa are diminished in size. 6.1 mm SL; 630×. 5) The mucosa of the midgut shows good integrity and organization, and the lumen contains moderate food residue. 6.3 mm SL; 250×. 6) The midgut is filled with disassociated cellular debris and the mucosa is fragmentary. Separated trunk muscle fibers are also visible. 8.5 mm SL; 250×. Symbols: Fg, foregut; K, kidney; L, liver; M, trunk muscle; Mg, midgut; N, notochord; R, food residue; T, transverse muscle coat of digestive tract; U, mucosa.

reported for a number of ungulates, primates, and birds (Harthoorn 1977) and in the swordfish, *Xiphias gladius* (Tibbo et al. 1961). The outstanding symptom is degeneration of skeletal muscle, presumably from acidemia from overexertion during intense flight and struggle in capture. Though the possibility cannot be entirely dismissed, capture myopathy seems an unlikely cause of the



FIGURES 7-12.—Histological comparisons of healthy (left) and emaciated (right) northern anchovy larvae.—Continued. 7) The trunk muscles cut in cross section above and below the notochord are compact. The foregut and midgut have mucosa of good thickness and integrity. 5.5 mm SL; 100×. 8) Trunk muscles are separated and uneven, the midgut is filled with disassociated cellular material, and the pancreas is severely disassociated. 5.5 mm SL; 100×. 9) Portions of the midgut, the pancreas, and the trunk musculature below the notochord all show good integrity. 5.0 mm SL; 250×. 10) Enlargement of Figure 8 for comparison of pancreas to that in Figure 9. 250×. 11) The foregut is regular and the trunk muscles are compact. The foregut is not yet expanded, and the midgut is not visible in the section. The remnant of the yolk sac, primarily periblast tissue, is prominent. 2.5 mm SL; 250×. 12) The midgut is a solid mass of necrotic debris. The notochord and trunk muscles are collapsed and irregular. The kidney is necrotic. 2.2 mm SL; 250×. Symbols: Fg, foregut; K, kidney; L, liver; M, trunk muscle; Mg, midgut; N, notochord; P, pancreas; S, spinal cord; U, mucosa; Y, yolk.

muscle deterioration observed in the northern anchovy larva. It is essentially a phenomenon of protracted struggle in large animals. In the case of the northern anchovy larvae, time and physical manipulation were minimized in capture.

Depletion of tissues arising from starvation seems a more likely cause of muscle deterioration. Love (1974), in summarizing depletion in (adult) fishes, states that ". . . when fish are starved the lipid reserves . . . decrease to a certain point beyond which the muscle protein is mobilized. As the protein decreases, the water increases, and this change is mainly brought about by shrinkage of the cells and a corresponding increase in the fluid between them." In conjunction with these findings it had been shown that extracellular spaces appeared in the musculature of Atlantic cod, *Gadus morhua* (Love et al. 1968), and American plaice, *Hippoglossoides platessoides* (Templeman and Andrews 1956). Deterioration of the musculature was a prominent effect following artificial starvation of early postyolk-sac northern anchovy larvae (O'Connell 1976) and of jack mackerel, *Trachurus symmetricus*, larvae (Theilacker 1978). Deterioration of musculature during starvation has also been observed in larval herring, *Clupea harengus*, and plaice, *Pleuronectes platessa* (Ehrlich et al. 1976).

Digestive Tract

In most larvae the long foregut was straight with a uniform lumen and a smooth surfaced mucosa of cuboidal or thick squamous cells (Figure 3; see also Figures 1 and 7). The foregut was considered anomalous if the profile was noticeably irregular in sagittal view. The mucosa usually also showed some variation in cell thickness and shape. In the more extreme cases the mucosa cells tended to be reduced to little more than the nucleus (Figure 4), and the lumen sometimes contained a few sloughed cells.

The midgut varied greatly in appearance, depending on the degree of longitudinal folding and transverse ridge development and on the plane of a particular section. Nevertheless, in most specimens a substantial lumen, sometimes containing food, and a simple mucosa of low columnar cells could be traced (Figures 5, 7, 9). Although the infranuclear portions of the cells were often narrowed and slightly separated, the supranuclear portions were always well joined.

The midgut was judged anomalous when little or no lumen could be traced, or when the traceable lumen contained a considerable bulk of loose nuclei and necrotic cellular debris, and the mucosa proper was fragmenting (Figures 6, 8, 10). In the worst case the midgut was a homogeneous mass of necrotic debris enclosed in only a basement membrane, with no trace of either lumen or mucosa (Figure 12). This specimen, which happened to be the smallest examined, also showed a severely collapsed notochord and degenerate musculature. The degree of organ development, including fully pigmented eyes, indicated that it had shrunken. Healthy specimens of comparable size, which still had unpigmented eyes, showed good notochord and musculature, and often a sizable remnant of the yolk sac (Figure 11). Shrinkage has been shown in laboratory starved larvae of both the Atlantic herring (Blaxter and Hempel 1963) and the northern anchovy (O'Connell 1976; O'Connell and Raymond 1970).

Whereas the muscle and foregut anomalies are at least logically acceptable as consequences of inadequate nourishment, interpretation of the midgut anomaly is problematical. In artificially starved northern anchovy larvae the midgut showed thinning and increased separation of cells, and the loss of some cells (O'Connell 1976), but not strong contraction followed by general fragmentation and necrosis of the mucosa as seen in some of the ocean-caught specimens. It may be, of course, that the symptoms were different because the laboratory and ocean situations were different. Laboratory animals were starved without ever having an opportunity to feed, whereas the oceanic larvae showing symptoms undoubtedly did have the opportunity to feed. Most in fact had processed food through the digestive tract, as indicated by the presence of supranuclear inclusion bodies in the mucosa cells of the hindgut, though the hindgut and the inclusion bodies were sometimes in a state of disintegration. Such inclusion bodies were never found in laboratory specimens deprived of food from time of hatching (O'Connell 1976).

Contraction and congestion resembling that seen in the midguts of the emaciated northern anchovy larvae from the ocean have been described for some other fishes, but they can be symptomatic of disease as well as of starvation. *Clupea harengus* larvae of 9-13 mm, for example, are vulnerable to a nematode that grows in the body cavity and deforms the gut, often resulting in occlusion of the lumen that blocks food intake and/or defecation (Margolis 1970). There are other nematodes whose larvae attack the gut walls of certain fishes, causing inflammatory and degenerative changes, including localized necrosis and infiltration of abundant lymphocytes (Margolis 1970). There are also protozoans, such as

Nosema anomala, which invade the intestinal wall of the young of the threespine stickleback, *Gasterosteus aculeatus*, and generate hypertrophied cells filled with its vegetative and reproductive stages (Lom 1970). Certain viral diseases produce degenerative changes that include necrosis and sloughing of intestinal epithelium (Yasutake 1975). On the other hand, starvation of immature salmon cause, among other things, marked atrophy of the stomach with degeneration of the epithelium, which ". . . could presumably be used for nourishment" (Love 1974). Starvation of

TABLE 1.—Numbers of northern anchovy larvae and other data by net tow for March 1977, off southern California. Number emaciated and standard length pertain only to sectioned larvae. See Figures 13 and 14 for tow locations.

Tow	Date	Hour	Temperature (°C)	Plankton volume (ml)	Number of Larvae		Mean standard length	Number emaciated		
					In tow	Sectioned		Severe	Moderate	Incipient
1	17	1530	13.2	1	0					
2		1750	13.8	5	9	6	4.6			
3		2210	13.5	4	33	7	4.0	1		
4	18	0825	14.2	2	9	5	5.0			
5		1035	14.5	2	9	5	4.9			
6		1440	14.7	3	14	6	6.4			
7		1910	14.7	3	68	6	5.4			
8		2340	14.8	2	47	6	4.7			
9	19	0350	13.7	3	54	6	4.5	3	1	
10		1010	15.2	4	7	7	4.9	3		1
11		1215	15.6	3	2	2	3.9		1	
12		1550	15.5	1	32	6	5.1			
[1]13		1600		8	[2]200	6	5.2			2
14		2215	14.6	11	43	6	4.7			
15	20	0005	13.4	4	24	10	6.7	4	1	2
16		0735	13.6	4	59	6	4.7			
17		1135	14.0	10	20	7	5.5			
[1]18		1205		3	15	6	4.2			
19		2045	15.0	7	70	6	5.5			
20	21	0005	14.9	4	65	7	6.5	4	2	1
21		2045	14.2	21	[2]400	6	5.0			1
22	22	1920	14.2	7	16	6	5.7			
23		2255	13.6	32	[2]350	7	6.0			
24	23	0945	14.6	6	40	6	4.2			
[1]25		0955		10	54	6	4.4			
26		1110	14.7	3	5	5	4.4			
27		2045	14.1	12	180	6	4.9			
28		2315	13.4	7	56	5	5.4		1	
29	24	1020	14.7	14	62	6	5.3			
[1]30		1030		8	67	7	5.3			
31		1440	13.7	7	8	6	5.4			1
32		1915	14.8	11	[2]200	6	4.7			1
33	25	0120	13.8	35	[2]300	6	4.9			
34		1550	13.1	14	97	7	4.8			
[1]35		1555		5	22	6	5.7			
36		2310	13.4	6	122	7	6.9			
37	26	0140	13.1	38	[2]250	6	7.1			
38		0345	12.7	10	19	6	6.6			
39		0550	12.3	33	4	4	12.5			
40		0730	12.8	17	0					
[1]41		0740		29	0					
42		0927	12.7	106	1	1	8.0			
43		1300	14.4	4	1	1	5.9			
[1]44		1325		21	1	1	12.2			
45		1620	14.1	1	0					
[1]46		1630		12	1	1	8.5			
47		1745	14.5	7	0					
48		2030	14.2	13	2	2	10.6			
49		2205	14.2	21	2	2	9.3			
50		2345	14.3	15	3	3	7.2		1	
51	27	0120	13.8	19	2	2	8.2			
52		0240	13.2	29	16	16	12.3			
53		0410	13.2	42	35	15	11.0		1	
54		0645	14.2	7	0					
55		1340	14.5	10	0					
56		1450	14.6	20	0					
57		1600	14.5	7	0					
[1]58		1610		30	0					
59		1839	14.1	27	5	4	9.8	1		2
60		2115	14.0	17	3	3	12.8		1	
61		2330	13.8	12	1	1	11.7			
62	28	0145	14.4	15	11	7	9.4			
63		0415	15.2	5	42	14	7.1			
64		0640	15.2	2	22	15	6.9	1		

[1] Taken at same location as preceding tow at almost twice the depth.
[2] Number estimated from count of a substantial fraction.

mummichog, *Fundulus heteroclitus*, up to 8 days resulted in a decrease in the quantity of lipid droplets in cells of the digestive tract and contraction of the intestine such that the lumen was small, sometimes scarcely traceable (Ciullo 1975). While these considerations suggest that disease could be the cause of the midgut anomaly present in certain of the ocean-caught northern anchovy larvae, starvation is the more tenable explanation because there was no evidence of parasites or pathogens in the hematoxylin- and eosin-stained specimens, and other anomalies in these specimens were consistent with demonstrated effects of starvation.

Other Organs

Deterioration was sometimes evident in other organs, particularly in the specimens with the most severe anomalies in the musculature and digestive tract. The pancreas and liver, for example, showed good integrity in most larvae (Figures 1, 9), but some showed an unusual degree of dissociation in these organs (Figures 8, 10), and in a few, both organs had undergone considerable lysis. The kidney ducts were intact in all specimens, but in a few the cells of the ducts were unusually thin, or necrotic (Figure 12). In several the mantle layer of the brain showed poor integrity, perhaps from a reduction of neuroglia.

Classification of Larvae

During the course of microscope examination, each larva was designated healthy, incipient emaciation, moderate emaciation, or severe emaciation. The three classes pertaining to larvae with anomalies are not rigorous, but they imply the following: incipient, slight looseness of the trunk muscles; moderate, obvious separation of the trunk muscle fibers, some irregularity of the notochord and possibly the foregut, strong contraction of the midgut, and sometimes a high incidence of hypertrophic cells in the midgut mucosa; and severe, obvious separation and hyalinization, and sometimes disarray, of the muscle fibers, notable irregularity in the profile of the notochord and foregut, depletion of foregut muscosa cells, and fragmentation of midgut mucosa, with a central core of dissociated and necrotic cellular debris. Of the 318 larvae sectioned, 26 were classified as severely or moderately emaciated, and another 11 were classified as incipient. These are listed by net tow in Table 1 along with the raw data for all tows. The larvae classified as incipient are included with the healthy rather than with the emaciated or "starving" group in the sections that follow.

Relation of Emaciated Larvae to Other Variables

Standard Length

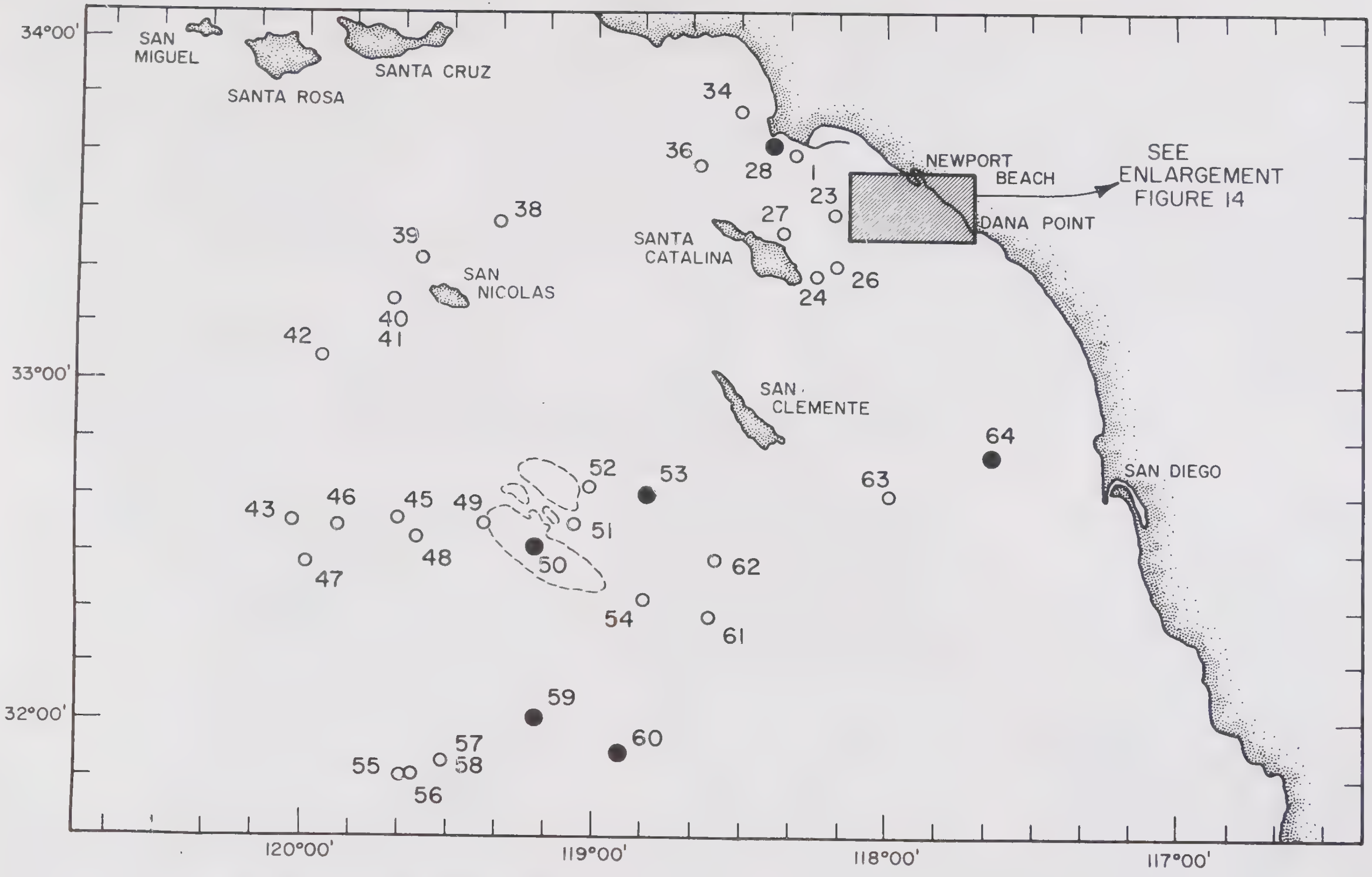
Emaciated larvae were all <10 mm SL and were distributed almost proportionately over the range 2-10 mm SL (Table 2). Larvae classified incipient were similarly distributed. In the lowest size category, 2.1-4.0 mm SL, only half of the 46 larvae examined had exhausted their yolk and become vulnerable to starvation. The emaciated individuals were part of this contingent. The absence of emaciated larvae in the categories above 10 mm SL may be a chance result of the relatively fewer numbers of larger larvae present in the tows, but there may also be some actual reduction in starvation effects at this size because of increasing lipid reserves with growth (Love 1974).

TABLE 2.—Standard length distribution of the northern anchovy larvae sectioned and examined and of those classified as emaciated or incipient.

Standard length	Number examined	Number emaciated	Number incipient
2.1- 4.0	46	6	3
4.1- 6.0	137	8	3
6.1- 8.0	60	8	3
8.1-10.0	30	4	1
10.1-12.0	26		1
12.1-14.0	14		
14.1-16.0	3		
16.1-20.0	3		

Geographical Distribution

More than half of the tows were spread over a large offshore area where abundance of northern anchovy larvae was generally low (Figure 13, Table 1) and where samples from six tows each contained a single emaciated larva. The remainder of the tows occurred in an area of a few hundred square miles off Newport Beach where larval abundance was high (Figure 14, Table 1) and where samples from four tows each contained several emaciated larvae. The fact that these four samples showed a high proportion of emaciated larvae, while others from nearby tows showed only healthy larvae, indicates that there was a contagious or patchy distribution of such larvae off Newport Beach.


34°00'
33°00'
32°00'
120°00'
119°00'
118°00'
117°00'
SAN MIGUEL
SANTA ROSA
SANTA CRUZ
SAN NICOLAS
SANTA CATALINA
SAN CLEMENTE
NEWPORT BEACH
DANA POINT
SAN DIEGO
SEE ENLARGEMENT FIGURE 14
34
36
28
1
23
27
24
26
38
39
40
41
42
43
46
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48
47
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62
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55
56

FIGURE 13.—The locations and sequence numbers of tows taken in March 1977 over the Southern California Bight, exclusive of the Newport Beach area. Open circles indicate tows from which all sectioned larvae were healthy, and dots indicate tows in which one of the sectioned larvae was emaciated. See Table 1 for data on tows.

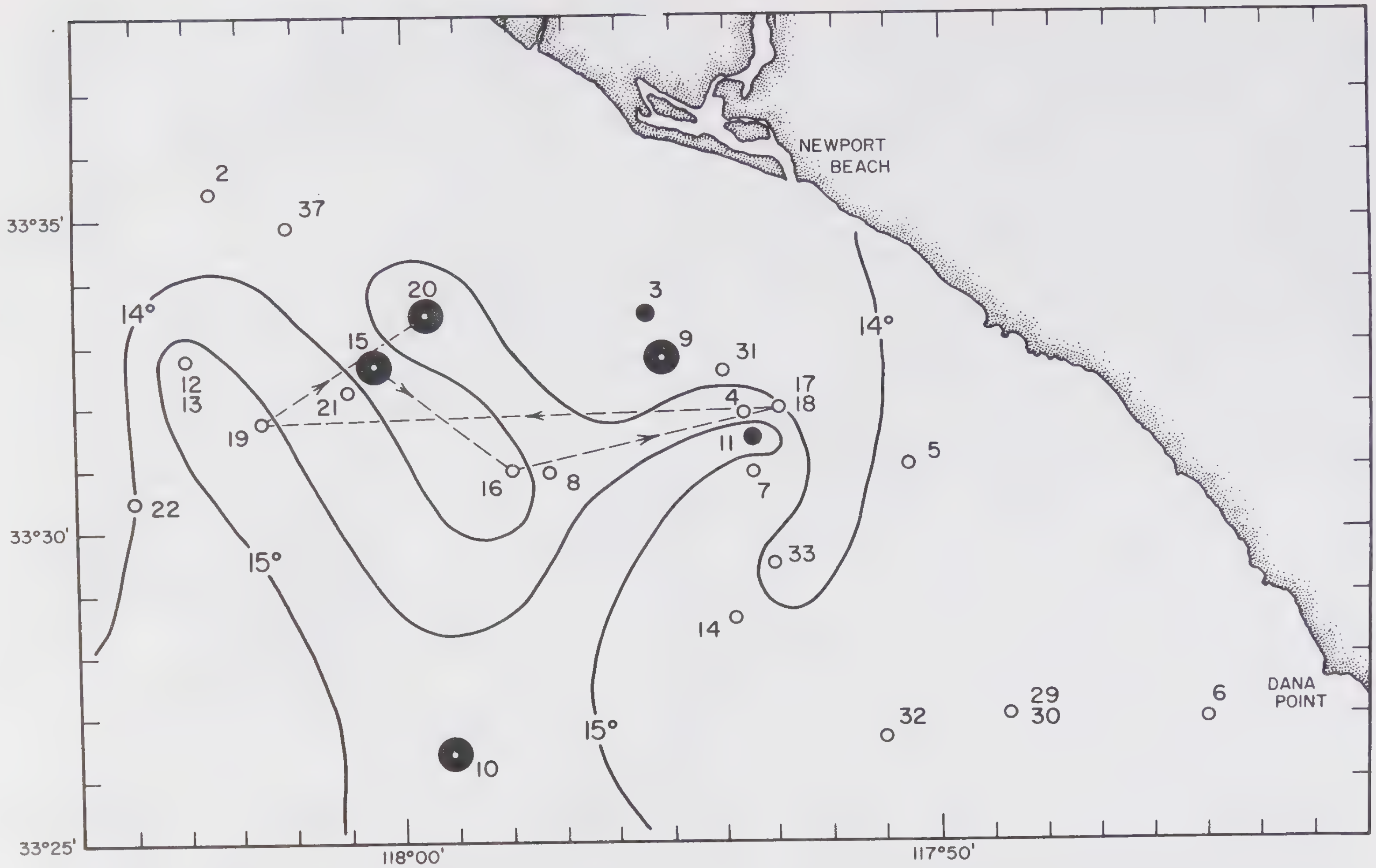
NEWPORT BEACH
DANA POINT
33°35'
33°30'
33°25'
118°00'
117°50'
14°
14°
15°
15°
2
37
20
15
21
12
13
19
22
3
9
31
4
17
18
11
16
8
7
5
33
14
10
32
29
30
6

FIGURE 14.—The locations and sequence numbers of tows taken in the Newport Beach area, southern California. Open circles indicate tows from which all sectioned larvae were healthy; dots indicate tows from which one of the sectioned larvae was emaciated; larger dark circles with open centers indicate tows from which most of the sectioned larvae were emaciated; 1° C surface isotherms show that there was considerable temperature variation in the area; and dashed line is the cruise track for one 24-h period, and it indicates that the presence of emaciated larvae (tows 15 and 20) was persistent over at least this time span. See Table 1 for data on tows.

The impression of "patches" of larvae in poor condition indicated by the histological samples from the Newport Beach area was further strengthened by subsequent examination of the unsectioned larvae remaining from all net tows. Figure 15 shows a random portion of tow 23, which contained over 300 larvae and produced only healthy larvae in the histological sampling. The specimens are full-bodied with good symmetry and are straight, or at worst gently curved. Figure 16 shows a random portion of tow 9, which produced a high proportion of emaciated larvae in the histological sampling. Several of these larvae have angular body bends, trunks and digestive tracts that are lumpy and sinuous, and heads often misshapen with loose or missing eyes. They also appeared to be less intensely colored by the fixing solution than the others. When viewed in toto, this and the other three tow collections of larvae that produced histologically poor samples were readily distinguishable from all others.

The emaciated larvae consititute a percentage of the number of larvae examined, but the magnitude of this percentage depends on the portion of the total samples that are considered (Table 3). The four tows with a high incidence of emaciation, considered by themselves, indicate 60% emaciated larvae within local patches. This drops sharply to 12% when coverage is expanded to a few dozen tows in approximately 200 mi^2 off Newport Beach, and to 10% when an additional 10 tows, rather widely scattered over the San Pedro Channel area are included (inshore set). By comparison, the pooled offshore samples (offshore set) which represent perhaps 6,000 mi^2, indicate 5% emaciated, and samples pooled for the entire cruise show an intermediate value of 8% emaciated.

Day and night subsets of the inshore and offshore sets show differences in both the available population and the percentage of emaciated larvae. The lower daytime catches imply that the population was less available during this period, probably because much of it migrated below the 20 m depth of the tows during the day and probably also because larvae have some success in visually avoiding the net during the day. As a simple binomial function, the 15% emaciated larvae for the inshore night group is significantly higher

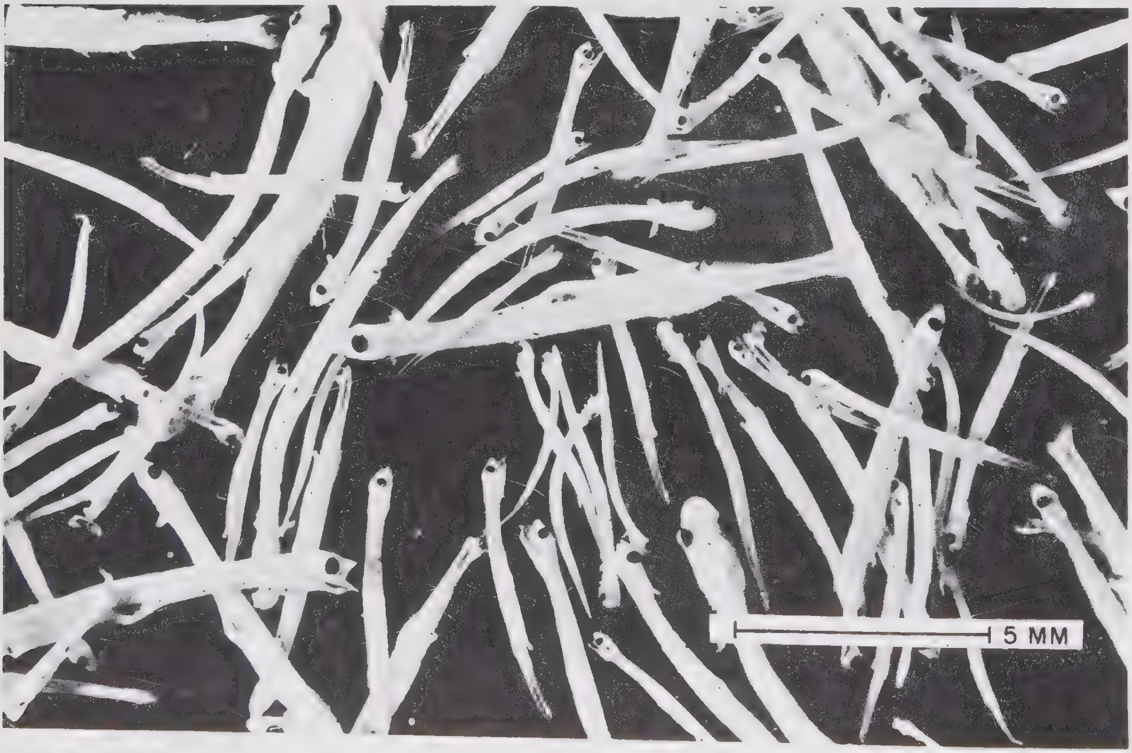

FIGURE 15.—A random portion of the northern anchovy larvae from tow 23, in which the larvae show generally good body form.

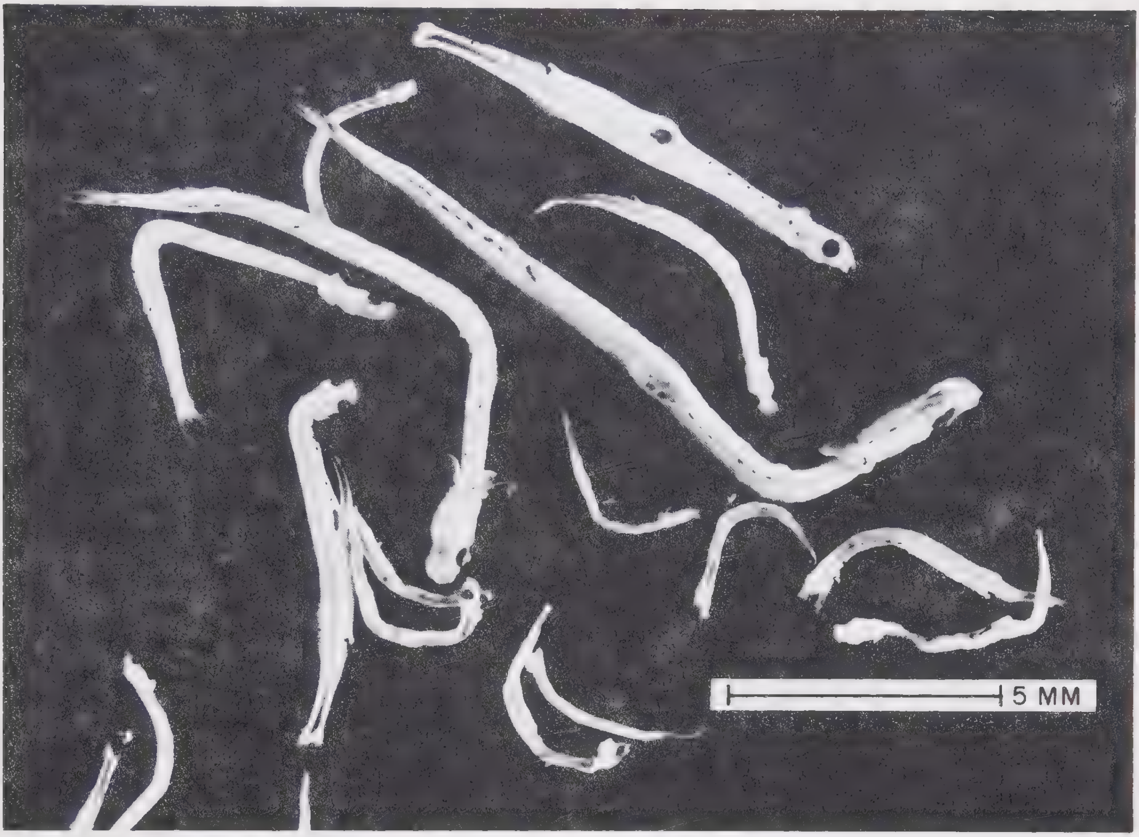

FIGURE 16.—A random portion of the northern anchovy larvae from tow 9, in which the larvae show generally irregular body form.

TABLE 3.—Percentage of emaciated northern anchovy larvae for different sample arrays.

Sample arrays	Number of tows	Larvae/ tow	Number of larvae examined	Number of larvae emaciated	Percent emaciated	95% confidence limits
Samples with high incidence of emaciation	4	37.5	30	18	60.0	±17.5
200 mi^2 coastal area includes above	27	77.1	165	20	12.1	± 5.0
Inshore set (tows 1-37):						
Day (0600-1800 h)	20	36.6	111	4	3.6	± 3.5
Night (1800-0600 h)	17	134.0	109	17	15.6	± 6.8
Pooled	37	81.3	220	21	9.6	± 3.9
Offshore set (tows 38-64):						
Day (0600-1800 h)	14	1.9	19	1	5.3	±10.0
Night (1800-0600 h)	13	11.2	79	4	5.1	± 4.8
Pooled	27	6.3	98	5	5.1	± 4.4
Total cruise pooled	64	50.0	318	26	8.2	± 3.0

than the other three subset percentages, but the obvious contagious nature of the distribution of these larvae casts doubt on the value of such tests. It is probably safer here to choose a lower percentage, such as the 8% for the entire cruise pooled, as representative, and assume that the observed subset differences are nothing more than sampling variation.

Surface Temperature

The tows with a high incidence of emaciated larvae were not associated with a given level of temperature, but it appears that they were located in an area of variable temperature (Figure 14). The 13° and 15° C tongues of water may have been basically persistent water masses, as Methot and

Kramer (1979) suggested, but the irregularity of the isotherms defining these tongues off Newport Beach implies local shifting of temperatures. Comparison of time as well as temperature differences along and adjacent to the cruise track for 20 March indicates, in fact, that notable temperature differences between closely located tows were probably more a matter of change over time than of static gradients between locations. Tows 15 and 20 are of particular interest because they both had a high incidence of emaciated larvae and were close together, but differed in temperature by 1.5° C. However, tow 20 was taken 24 h later than tow 15, and the thermograph record showed that the higher temperature applied to tow 15, as well as to the tow 19 and tow 20 positions, at the later time. Such short-term temperature shifts indicate that there was water mass instability or movement in the area.

Plankton Volume

Plankton volume averaged appreciably lower for the four tows with a high proportion of emaciated larvae than for either the inshore or the offshore set of tows (Table 4). The average number of larvae was also relatively low in these four tows, being about half the average for all tows off Newport Beach, or in the San Pedro Channel area (inshore set). Number of larvae and plankton volume, in fact, tend to be associated for the inshore set (Figure 17), and while the four tows with high incidence of emaciated larvae do not show the lowest values, they are among the tows with low values.

Plankton volume did not relate to temperature in the inshore area, but there were some interesting changes with time (Figure 18). From 17 March to midnight of 20 March all volumes were 11 ml or less. This includes the four tows with a high incidence of emaciated larvae, one of which (tow 20) was the last taken in this time period. Twenty-four hours later tow 21, the first tow with a markedly higher volume (21 ml), was taken at a nearby position (Figure 14). Three more tows of progressively higher volume were taken during night hours over the next few days, but there were also several tows with lower volumes (3-14 ml) taken during this period, some at night. This pattern indicates that there was a striking change in the plankton regime off Newport Beach starting on 21 March, with volume tending to be higher, especially at night, than it had been during the preced-

TABLE 4.—Mean plankton displacement volume (milliliters) for different sample arrays in the study of northern anchovy larvae off southern California.

Item	No. of tows	Larvae/ tow	Plankton Volume/ tow	Plankton SD
Samples with high incidence of emaciation	4	37.5	3.8	0.5
200 mi² coastal area includes above	27	77.1	8.3	9.3
Inshore set includes above	37	81.3	8.7	9.0
Offshore set	27	6.3	19.7	20.1
Total cruise	64	50.0	13.3	15.6

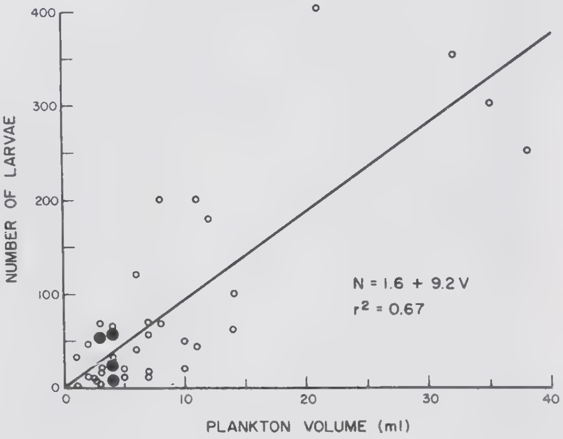

FIGURE 17.—The regression of number of anchovy larvae on displacement volume of plankton (larvae excluded) for the inshore tows, 1-37. The solid circles indicate the four tows with a high incidence of emaciated larvae.

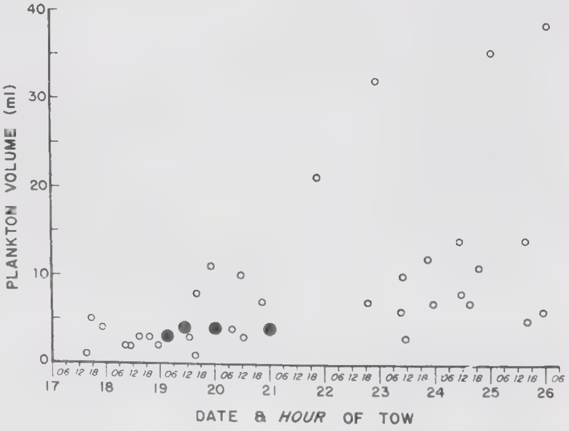

FIGURE 18.—Displacement volume of plankton on date (March 1977) and hour of tow. Dots indicate the four tows with a high incidence of emaciated larvae. Dates are in bold type and located at midnight points on the hour scale.

ing few days, when the tows with a high incidence of emaciated larvae were taken.

DISCUSSION

The most significant result of this study is that northern anchovy larvae showing symptoms indicative of starvation were indeed found in the ocean and were thus identified on the basis of their individual appearance. The emaciated condition of these larvae is very similar to that induced in laboratory animals by total food deprivation (O'Connell 1976), which implies that circumstances of insufficient food were responsible for their occurrence in the ocean, especially where samples contained many such larvae, as off Newport Beach. Other causes are possible, and one of the most obvious is discharge from sewage outfalls in the area. However, the discharges are now diffused rapidly and in general appear to be harmless and perhaps even beneficial to nearby young and adult fish (Southern California Coastal Water Research Project[3]).

Zones of insufficient food might well have existed in the Newport Beach area at the time of the survey. The variations in both temperature and plankton volume, which were clearly dynamic in nature, indicate that there was appreciable water mass movement or instability, and such conditions can alter plankton abundance. Lasker (1975, in press) found, for example, that phytoplankton blooms believed to be advantageous for first feeding anchovy larvae were variously dissipated and suppressed as the water column became unstable in turbulent weather and sea conditions. In the present study the time sequence of plankton volume change off Newport Beach shows the possibility that water with relatively low plankton levels and "patches" of emaciated larvae was being replaced by water with greater plankton abundance, in which larvae were also more abundant and generally healthy.

Although the occurrence of zones of insufficient food is a reasonable hypothesis in regard to the "patches" of emaciated larvae off Newport Beach, it is not a plausible explanation for some of the other samples, where occasional emaciated individuals occurred among abundant healthy larvae. It can only be surmised that in any location, and despite generally good conditions, there will be some instances of starvation through detrimental combinations of genetic constitution, accident, and chance failure to capture food.

If circumstances of poor food availability are produced by water mass activity, as suggested above for the Newport Beach area, they are likely to be more or less transient phenomena, which raises the question of short-term susceptibility of northern anchovy larvae. Immediately after yolk absorption, northern anchovy larvae will survive only a day or two without food (Lasker et al. 1970), and they will show visible effects before dying (O'Connell 1976). Protein components are quickly affected because early postyolk-sac fish larvae have negligible lipid reserves (Ehrlich 1974), though such reserves obviously increase with growth and become a buffer against insufficient food (Love 1974). Even so, northern anchovy larvae of relatively large size, 35 mm SL, survived only 2 wk, on the average, after feeding was stopped, and during this period the average lipid content of living larvae was declining while mortality in the population was rising, with smaller individuals dying sooner than larger ones (Hunter 1976a). Since larvae examined in the present survey were appreciably smaller than the above, thus having lower lipid reserves, the signs of emaciation could have resulted from relatively few days of insufficient food.

Most of the larvae showing histological signs of emaciation in this study also showed signs of previous feeding, not by the presence of food residue, but rather by remnants of eosinophilic inclusion bodies in the hindgut mucosa cells. The starvation and previous feeding indications are not incompatible. Laboratory feeding studies have shown that growth, lipid content, and survival all decline quickly under limited or discontinued feeding (O'Connell and Raymond 1970; Hunter 1976a), and it is probable that histological signs of deterioration would also appear quickly, especially in early larval stages.

If, as proposed by Hjort (1914, 1926), the level of mortality suffered by the early feeding stages of fish populations is a decisive component of the prerecruitment mortality, some measure of that mortality should be a useful indicator of ultimate year class success. The proportion of larvae observed to be starving may be one such useful indicator: It is directly visible, and it may reflect a substantial part of total daily mortality. Zweifel and Smith (in press) have estimated average daily population abundance of larval anchovies by length and region for the 1967 through 1975 California Cooperative Oceanic Fisheries Investigations net tow data, and length dependent mortality rates were calculated from the abundance estimates. For larvae of 7.5 mm SL, which approximates the median length of those showing symptoms of starvation in the present study, the estimated average daily mortality rate in the San Pedro Channel area was 21%. If it is assumed that all larvae showing symptoms will die directly or indirectly from starvation, the observed 8% with symptoms in the March 1977 survey could indicate a net daily mortality from starvation of 8%, which is 40% of the average total daily mortality for this length group. If starvation tends to contribute this substantially to total mortality, variations in the proportion of larvae observed to be starving may relate reasonably well to the magnitude of ongoing total mortality and consequently to recruitment from the year class.

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[3] Southern California Coastal Water Research Project. 1978. The effects of the ocean disposal of municipal waste. Summary Report of the Commission of the Coastal Water Research Project, June 1978, 27 p. Filed at 1500 East Imperial Highway, El Segundo, CA 90245.

How well the proportion of starving larvae from a given sampling in 1 yr will predict the eventual recruitment of that year class will only be evident from correlation of the two variables for at least a few years. As for 1977, with a northern anchovy "starvation ratio" of 8%, there were indications that recruitment would be good. The winter and early spring were relatively mild, a condition conducive to development of high density patches of larval food organisms, particularly from dinoflagellate blooms (Lasker in press). Growth rate of northern anchovy larvae was also shown to be above average in the San Pedro Channel area for March 1977 (Methot and Kramer 1979). The above average growth rate may have been valid for much of the population developing in the region without applying to the patches of emaciated larvae, which were taken at different locations than the growth samples. Estimates from recent catch data indicate that the 1977 year class is of moderate size, as compared with the large 1976 and 1978 year classes and the small 1974 and 1975 year classes (J. S. Sunada[4]). Thus, to the extent that 8% starving larvae is a reliable estimate of that parameter for 1977 and to the extent that the parameter is associated with recruitment, both higher and lower occurrences of starving larvae are likely possibilities from future surveys.

Reliability of the estimate of starving larvae is probably reasonably good for 1977 in that tows were most concentrated in a region of high abundance, but reliability in future sampling efforts could probably be improved by more diligent stratification in respect to population distribution. In addition to sampling at more than one point in time, an effective strategy might be to expand sampling in several areas that show high abundance, particularly of larvae under 10 mm SL, along a preplanned survey track. Expanding sampling in this way would likely result in a quantity of samples that would be formidable if analysis is entirely dependent on histological or physiological parameters. The distinctive appearance of the aggregated larvae from those few tows of the present survey that contained predominantly emaciated larvae, however, suggests that histological analysis can be greatly reduced.

Assuming that starvation of any consequence will occur in patches, a stereomicroscope scan of the total aggregation of larvae from each tow should suffice for the identification and enumeration of such patches, with histological processing reserved for selected verification. Undoubtedly some of the starving larvae that occur as scattered single cases would be missed under such a procedure, but this should have little effect on the overall estimate.

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Eddies of the California Current System: Physical and Ecological Characteristics

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INTRODUCTION

This paper reviews eddies and their ecological effects in the California Current System (CCS). The importance of eddies lies in the physical properties of eddy motion and the effect on what we can identify to be systematic in flow patterns and in patterns of organism distribution. The Southern California Eddy (SC Eddy), which owes at least its character and perhaps its existence to the island and bank system off southern California, receives special attention because it is the most resolvable and ecologically significant eddy known in the CCS.

Many terrestrial populations as well as littoral and planktonic marine communities may prove to be continuously or temporarily maintained by eddy processes in otherwise marginal habitats. The fate of manmade products (MacGregor 1974) and their effect on island coastal and oceanic populations are also in part determined by the flow perturbations of the CCS. Formation of eddies in the flow is of particular interest since organisms and substances in transit become rather differently distributed in space and time in gyre-like circulations. Concentrations of organisms and substances are maintained in eddies at higher levels and for longer periods, their trajectories are markedly different, and populations which would not otherwise interact are juxtaposed. Recirculation by eddies further affects such local environmental conditions as temperature and nutrient distribution in the water, and humidity, temperature, and cloud cover in the atmosphere. My purpose is to give examples of eddy circulation—both free and stationary—and to show that large eddies are more a rule than an exception in the CCS, particularly in the Southern California Bight (SC Bight). I wish also to support the hypothesis that eddies larger than 10 km in diameter and longer than a week's duration have a major role in sustaining the high biological productivity which is characteristic of the inshore 200 km of the CCS.

Baroclinic eddies, meaning those identifiable from their effect on the mass field, have the interesting property of deforming the observable density field. A cyclonic eddy of sufficient size and intensity exhibits a detectable dome in surfaces of constant density to the depth where the eddy motion vanishes. This signals that the thermocline layer, which marks a sharp increase in water density with depth, has risen and displaced surface mixed-layer water, which is stripped of nutrients and usually poor in phytoplankton as well. In regions such as the CCS, where the thermocline is nutrient-laden and close to the bottom of the photic zone, this elevation results in a vertical flux of nutrients which affects growth of phytoplankton stocks. The new availability of nutrients is augmented and sustained by upwelling (here meaning upward flow across the eddy's density surfaces) in and near the eddy center and by mixing and stripping from shear flow across the thermocline layer of the eddy. Additional nutrients are supplied in episodic fashion during storm activity long or severe enough to erode the dome, with its relatively exposed pate (*e.g.*, Blackburn 1966). If such an eddy is associated with a boundary, it will also collect and conserve populations and nutrients washed down from the boundary layer of the obstacle. Seed populations in such eddies appear to respond to this major niche modification by increasing their production and biomass and thus rapidly create new sequences of community structure (*e.g.*, Sargent and Walker 1948). Closer examination of biological effects of eddies seems warranted to determine, for example, whether eddy processes can affect production and survival of the commercially and ecologically significant anchovy, *Engraulis mordax*. This may occur by eddy effect on phytoplankton community structure or on productivity, both important factors in determining survival of the large numbers of anchovy spawned in the region (Lasker 1975, Smith 1978).

THEORY AND PHYSICS OF EDDY FORMATION

A fluid of a given viscosity impinging on an obstacle produces eddies if the obstacle is large enough or if the flow is fast enough. These eddies can be stationary, "attached" to the lee side of the obstacle, or, with increased flow or obstacle size, may be shed in a series similar to a von Kármán vortex street. A vortex street, in air or water, extends as a series of paired eddies downstream from the obstacle. There exists a large body of theory on transitions from laminar flow to stationary eddy formation to eddy street formation for simple obstacle geometries in ideal fluids. Island profiles and ocean flow are neither simple nor ideal, however. In view of the complex and hazily perceived behavior of island-ocean systems of the Pacific, it is scarcely worth reviewing theory beyond the degree to which it has been helpful in describing large eddies in the sea. Irregularities in the flow impinging on the obstacle in question cause part of the complexity. In addition, interaction of small perturbations with larger ones, changes in depth and degree of density stratification, and irregular geometry of islands and shoals all contribute to the difficulty of verifying theory by measurement.

Van Dorn *et al.* (1967) investigated circulation downstream from two small, mid-Pacific islands using direct current measurements. They described from somewhat limited observations what appears to be stable shedding of eddies in the wakes of the islands. Choosing a relatively simple system, Barkley (1972) examined flow past Johnston Atoll, a small, mid-Pacific barrier, using direct current measurements by drogues and his ship's drift. He found remarkable agreement between observed current patterns and von Kármán's physical-mathematical model of flow past long cylinders, considering the simplifying assumptions that were necessary (constant impinging current velocity, no vertical motion, and constant wake characteristics). His observations demonstrated perhaps the first obstacle-induced vortex street to be detected in the sea (Fig. 1). As Barkley pointed out, islands in clusters may act as a single obstacle to flow and extend wake effects far beyond that expected for the sum of the single islands. Also, a small change in speed or direction of the impinging current may affect not only the partitioning of energy in the system but also distributions of physical, chemical, and biological properties within island clusters and for hundreds of kilometers downstream.

Patzert (1970) fitted a complex model of flow (the Rankine vortex; Rouse 1963) to the observed structure of a frequent free-eddy phenomenon west of the islands of Hawaii, although the impinging flow and obstacle geometry there is correspondingly more complicated than in the Johnston Atoll case. In this instance the ocean responded to atmospheric forcing. Impingement of the trade winds on the profile of this high island group evidently created vortices or jets in the wind, which caused eddy formation in the water.

In a study of subsurface flow past island groups, White (1971a, 1971b, 1973a, 1973b) examined the wake of the Equatorial Undercurrent (or Cromwell Current) downstream from the Galapagos island group, which is comparable in scale to the Hawaiian island group. The unique position of the Galapagos, on the equator and obstructing an east-flowing current, suggested that the observed meanders in the flow constituted a barotropic Rossby wake, which differs from a von Kármán street in that it is time-independent and owes its existence to variations of the earth's rotation with latitude as well as to the presence of an obstacle and impinging current. Due to the usual vagaries of the impinging undercurrent, White could not distinguish between

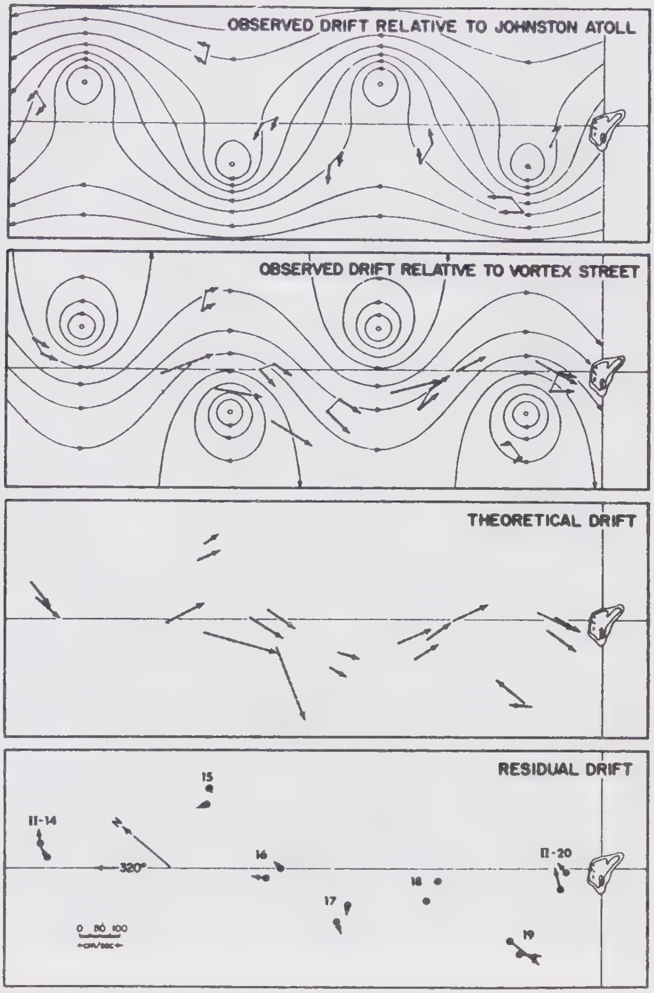

OBSERVED DRIFT RELATIVE TO JOHNSTON ATOLL
OBSERVED DRIFT RELATIVE TO VORTEX STREET
THEORETICAL DRIFT
RESIDUAL DRIFT
15
11-14
320°
16
II-20
18
17
19
0 50 100
cm/sec

FIGURE 1. *Eddies in the wake of Johnston Atoll (Barkley 1972, fig. 3). Streamlines were derived from von Kármán vortex street model fitted to direct current measurements (arrows). Degree of success of the model is evident from comparison of the two lower panels.*

wake mechanisms. However, as the Rossby wake phenomenon requires an eastward flow, it is unlikely to occur in the flow past islands of the Californias (Baja California, Mexico and California, U.S.A.) because the impinging currents usually have no eastward component.

An obstacle is not a prerequisite for generation of surface eddies in the ocean. Barkley (1968) was able to account for a variety of observed flow patterns in the open-ocean boundary between the Kuroshio and Oyashio Currents by their resemblance to a type of flow consisting of two vortex streets lying side by side. In this instance, the vortices were apparently generated by the convergence of the two currents in the absence of fixed boundaries. That baroclinic eddies can be independent of islands, coasts, or strong current convergences has not been demonstrated, yet various studies confirm their commonplace occurrence in the open sea in general (*e.g.*, Bernstein and White 1974), and in the CCS in particular (Sverdrup and Fleming 1941, Wyllie 1966, Bernstein *et al.* 1977).

In the vicinity of island systems of the Californias, we must expect that a combination of effects of wind, current, and topography must be invoked to understand patterns of circulation (Pavlova 1966, Reid 1965). The flow impinging on the islands is as complex as island/bank

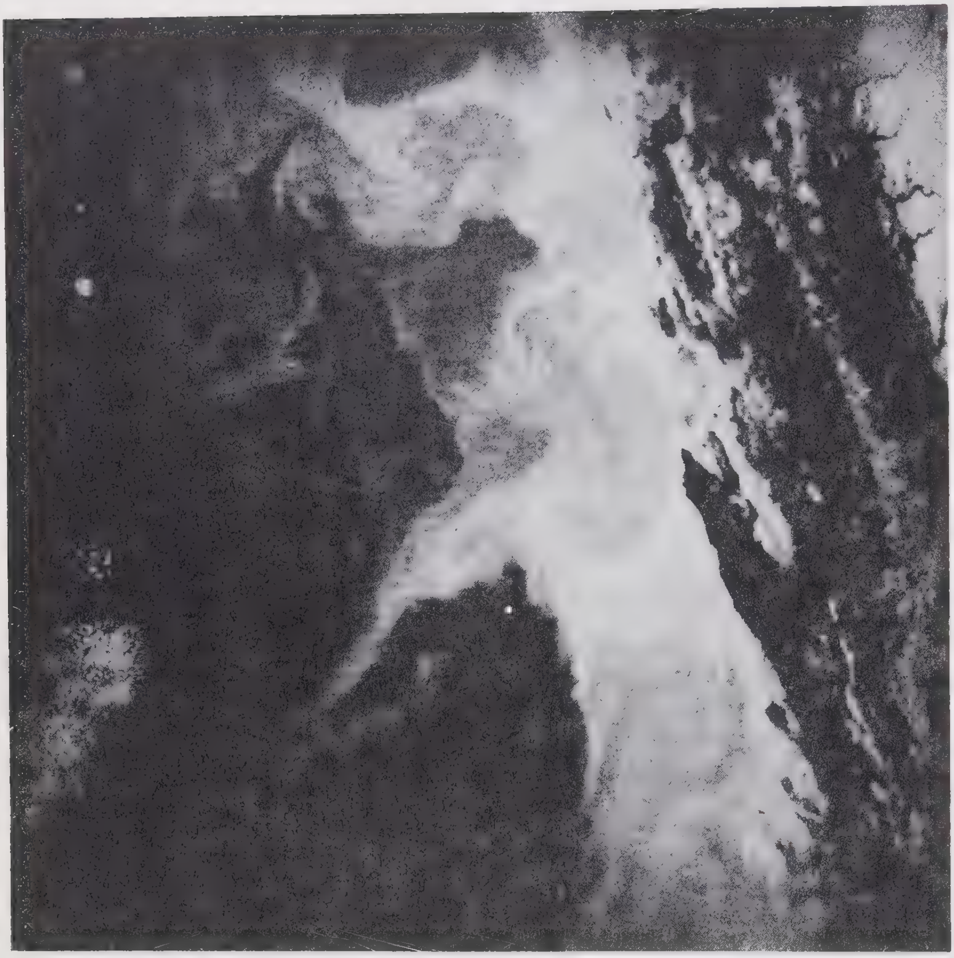
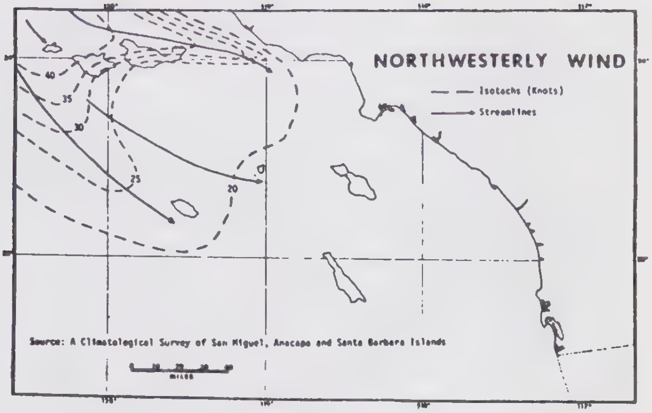


FIGURE 2. *Satellite photograph of sea-surface thermal patterns off California on 14 June 1975 (NOAA-3 satellite). Lighter shades represent cooler surfaces (Scripps Institution of Oceanography, Remote Sensing Facility).*

topography. Wind patterns exercise significant control, on the large scale, in producing the impinging flow and, on a local scale, in augmenting the perturbation of flow by the island and bank complex. Local winds are in turn affected by the islands and coastline. It is easy to understand why no simple theoretical treatment of the flow in this region can consistently account for observed current patterns downstream of the islands and banks of the Californias.

WIND

Wind stress on the sea surface is the primary source of the ocean's surface currents. The main theoretical approaches employed to account for the ocean's response to varying wind stress are those of Ekman (1905) and Sverdrup (1947), which, respectively, relate upper layer flow to temporal change in wind stress on the sea surface, and total water transport to spatial gradients of wind stress. These models have been applied to the California Current System. Bakun



Source: A Climatological Survey of San Miguel, Anacapa and Santa Barbara Islands

FIGURE 3. *Wind speed and direction over the SC Bight during northwest winds (U.S. Dept. Interior 1978, p. 65).*

(1973), for example, used Ekman's theory and computed upwelling intensity and timing regionally along the coastline of the Californias and farther north. These indices apply over distances too great to resolve localized phenomena. They may, however, be quite useful together with satellite thermal imagery in identifying regions and times of eddy activity associated with upwelling, should they prove to be commonplace. Sverdrup and Fleming (1941) found such eddies at the edge of an upwelling zone off Point Conception. Such an event appears again in a satellite photograph of thermal patterns in the sea off central California (Fig. 2). A cold plume and eddy extend seaward from a coastal upwelling zone, and the lower limb of a still larger eddy or meander is apparent—activity at least qualitatively similar to the upwelling edge-eddy found by Sverdrup and Fleming 42 years earlier off Point Conception.

Winds which affect local processes in the ocean off the Californias are predominantly out of the northwest and reach maximum velocity at a distance of about 200 km off the southern California coastline (Reid *et al.* 1958, Nelson 1977). Munk (1950), on the basis of his Sverdrup-based model of wind-driven circulation, found the offshore maximum in downcoast California winds to be consistent with the southward offshore flow and northward near-shore flow that seem to be prerequisites for strong SC Eddy development. Munk's meridional solution of the wind model also exhibits the weak and variable character of the main California Current.

In a more recent application of Sverdrup's theory, Nelson (1977) analyzed monthly mean values of wind stress in one-degree squares of latitude and longitude using surface wind observations from ships. This sampling grid was smaller (about 100 km) than those previously used for such wind studies, but still marginal for single eddy detection. His transport calculations from mean wind stress fields show flow directions consistent with the offshore equatorward transport of the California Current, near-shore poleward transport of the Countercurrent, and patterns south of Point Conception that are consistent with the SC Eddy.

The distribution of wind speed and direction over the region of the Channel Islands during northwest wind conditions is shown in Figure 3 (U.S. Dept. Interior 1978). It exhibits a two-jet system, consistent with wind retardation by the Northern Channel Islands of a single jet impinging from the north. High wind zones also are characteristic west and southwest off Point Conception (Reid *et al.* 1958, Allan Hancock Foundation 1965), but their role in eddy genesis is unassessed.

Sverdrup and Fleming (1941) discuss the possibility of coupling of atmospheric and oceanic eddies and raise the question of whether oceanic eddies are generated by the inherent ocean

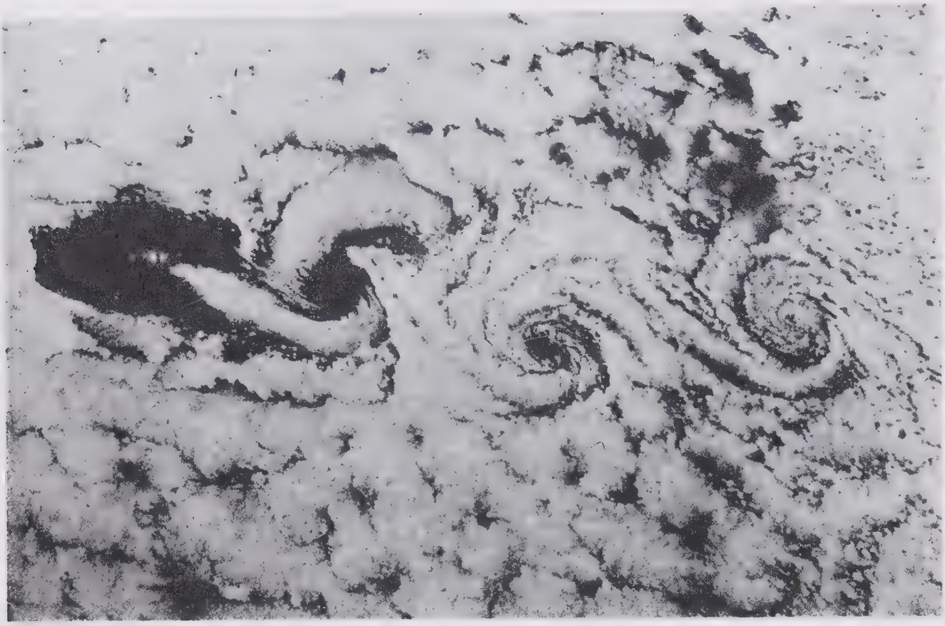


Figure 4. *Vortices in the atmospheric wake of Guadalupe Island off Baja California from Skylab on 6 September 1973 (NASA photograph SL-3*#121-2371).

current characteristics or are secondarily impressed on the ocean by the atmosphere. That this can happen elsewhere was shown by Patzert (1970), as noted above. Except for an eddy detected in the wind shadow of Cedros Island by Scripps Institution of Oceanography (SIO 1962), wind-induced ocean eddies have not been shown to occur in the CCS, although it is likely that they do occur.

Reports of atmospheric perturbations due to islands, and of von Kármán-like vortex wakes in particular, have been well documented in recent years. This is due, as Barkley (1972) notes, to "a special combination of circumstances: the wind, an obstacle, the right kind and quantity of cloud cover at the proper level, and a satellite overhead taking pictures; all must be present." Figure 4 is one such picture. Guadalupe Island is shown as seen from the orbiting Skylab satellite in September 1973. The cloud patterns clearly show a vortex street in the atmosphere downwind of the island. Such vortex wakes and other types of eddies are apt to be common in both ocean and atmosphere. Berger and Wille (1972) and Chopra (1973) review these phenomena and their dynamics. Additional examples of atmospheric flow perturbations by islands, and further discussion of their characteristics, are provided in Chopra's (1973) review of island effects on oceanic and atmospheric flow as known through 1970. Of obstacles in the CCS, only Guadalupe Island receives direct mention, but Chopra also reports effects of both smaller and larger islands which show that obstacles of virtually any size may produce systematic flow deviations. When the proper observations have been applied in the CCS, eddies are virtually always detected. Closer inspection of eddy systems may reveal that local coupling of atmosphere and ocean is responsible for the free eddies and meanders of the CCS as well as the previously established large-scale atmospheric coupling to which the main California Current owes its existence.

CALIFORNIA ISLAND AND BANK OBSTACLES

The islands and banks of the Californias are large enough relative to the impinging flow to induce or modify eddies of baroclinic scale. In full detail, the island/bank/basin topography of the Californias surpasses the complexity of most continental shelf systems of the world, leading Shepard and Emery (1941) to classify it as a "continental borderland," to distinguish it from ordinary continental shelves. The 100-m depth contour roughly describes a major break in the shelf slope (Emery 1958). At this depth, the northern group of Channel Islands (San Miguel, Santa Rosa, and Santa Cruz) may be considered a single obstacle to the flow, whereas the islands of the southern group (Santa Catalina, San Clemente, Santa Barbara, and San Nicolas) act individually. At the 500-m depth contour, the northern island group, San Nicolas, the Santa Rosa-Cortez Ridge, and Cortez and Tanner Banks act as a somewhat leaky, 200-km extension of the coastline north of Point Conception; as such, they would act on eddies the size of the SC Eddy. The direct effects of the California island and bank systems on flow have not been quantitatively specified in the literature.

It should be noted that islands and other obstacles to flow in the CCS can induce upwelling that is independent of wind. A theoretical treatment of eastern boundary currents by R. S. Arthur (1965) identified the importance of change of flow vorticity to upwelling in the boundary layer downstream of westward obstructions to southward flow in the CCS. Where the thermocline and nutricline are shallow, the result of such upwelling is cool, enriched water at the surface south of such promontories (Reid *et al.* 1958).

Examples of records exhibiting eddy patterns from direct current measurements near California islands are shown in Figure 5. Drogues released at 10-m depths were tracked in the Southern Channel Islands (Panel A). The circular trajectories shown were downstream of San Clemente and Santa Catalina Islands and depict eddies with diameters somewhat greater than 30 km and circuit times of about 3 days at 10 cm/sec. These eddies were probably caused by flow perturbation by the islands since the measurements were made under calm wind conditions (SIO 1962). On the other hand, the eddy defined by drogue trajectories near Cedros Island (Fig. 5, Panel B) was probably caused by wind forcing; northwest winds impinged on Cedros and Bahía Sebastián Vizcaíno during the measurement period. This 30-km eddy was located on the edge of the wind shadow of Cedros (labeled "calm area"), and may be the only documented case in the CCS of the wind's role in eddy genesis.

On a larger scale, eddies can be detected in the lee of the Channel Islands and banks during an offshore wind from thermal image patterns of the sea surface photographed by satellite (Fig. 6) the day before it photographed the patterns shown in Figure 2. The downstream eddy and meander patterns range from 30 to 100 km in diameter, and an eddy (< 30 km) appears near an upwelling zone off northern Baja California. Upwelling and eddy activity were apparent north of Point Conception, as well.

The effects of islands on flow as described for somewhat simpler systems elsewhere thus apply to the California Islands and associated banks, as well; they are capable of generating and shedding eddies of a variety of sizes. They may also alter the eddy patterns of the impinging flow by attenuating small eddies and deforming large ones.

EDDY PATTERNS OF THE CALIFORNIA CURRENT SYSTEM

It is likely that eddies, or eddy-like motion, impart to the flow of the California Current its characteristic large variability, in which excursions from the mean flow are at least as large as the mean flow itself. Flow is usually treated as the net motion resulting from superimposition of three main components: that due to, or balanced by, the internal distribution of mass (baroclinic mode); that due to wind stress on the sea surface, a barotropic mode under changing wind

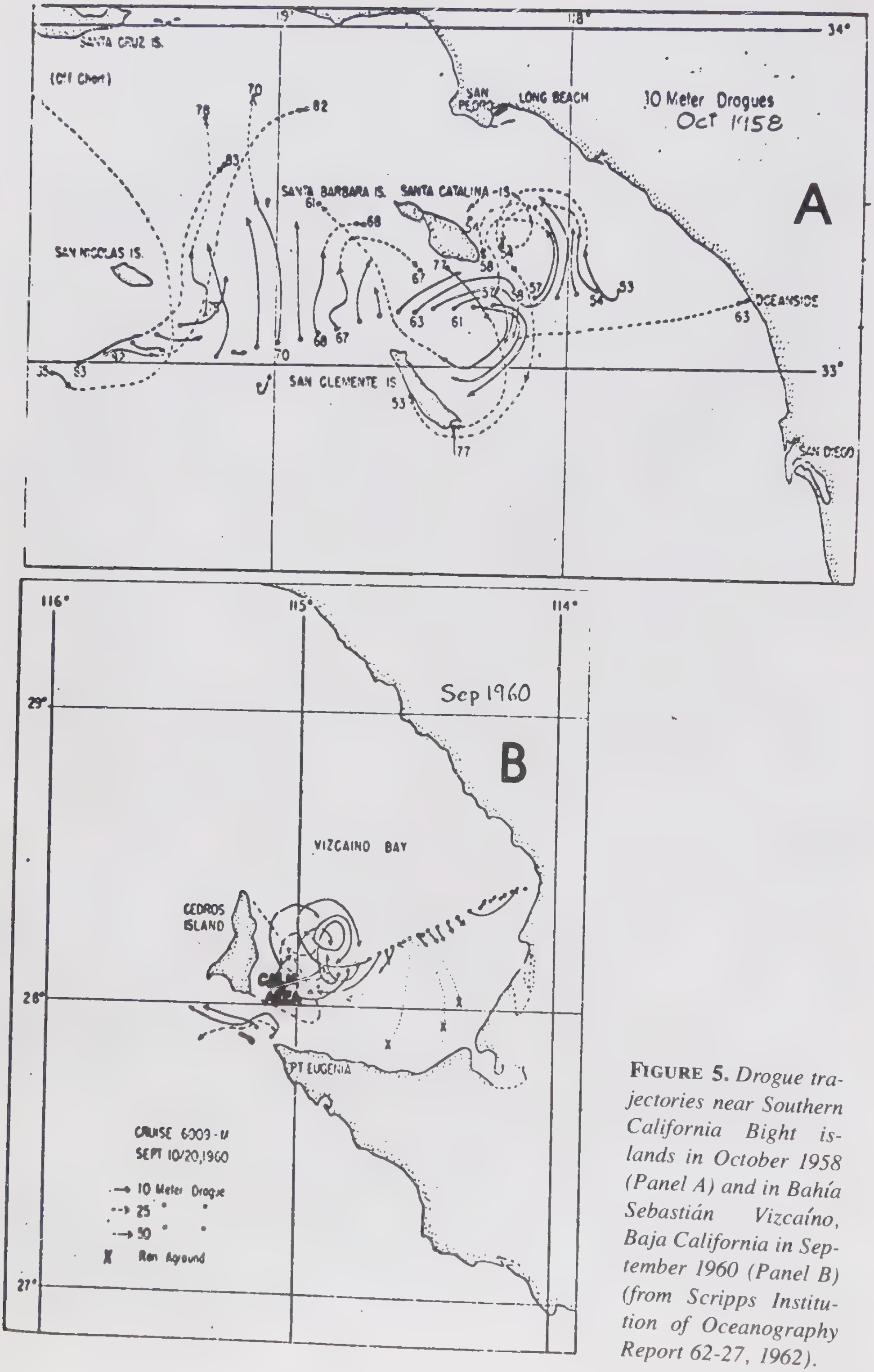

119°
118°
34°
33°
SANTA CRUZ IS.
SAN PEDRO
LONG BEACH
10 Meter Drogues
Oct 1958
A
SANTA BARBARA IS.
SANTA CATALINA IS.
SAN NICOLAS IS.
OCEANSIDE
SAN CLEMENTE IS
SAN DIEGO
116°
115°
114°
29°
28°
27°
Sep 1960
B
VIZCAINO BAY
CEDROS ISLAND
PT EUGENIA
CRUISE 6009-U
SEPT 10/20,1960
10 Meter Drogue
25 " "
50 " "
X Ran Aground

FIGURE 5. *Drogue trajectories near Southern California Bight islands in October 1958 (Panel A) and in Bahía Sebastián Vizcaíno, Baja California in September 1960 (Panel B) (from Scripps Institution of Oceanography Report 62-27, 1962).*

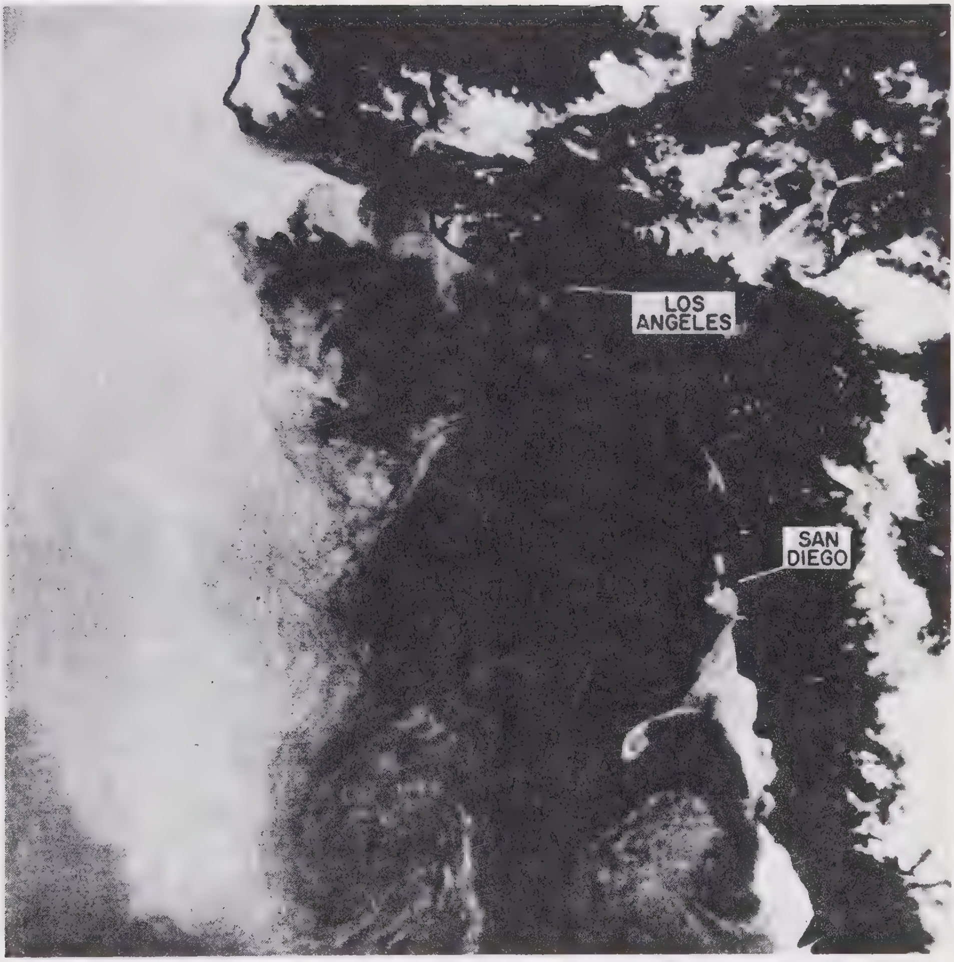


FIGURE 6. *Satellite photograph of sea-surface thermal patterns in the Southern California Bight on 19 September 1979 (NOAA-6 satellite). Lighter shades represent cooler surfaces (Scripps Institution of Oceanography, Remote Sensing Facility).*

conditions; and that due to tides and other cyclic internal motions, also barotropic. Direct determinations of currents are sensitive to all components, whereas currents depicted from the internal mass field (*i.e.,* from a spatial array of depth-integrated density profiles derived from temperature and salinity measurements) reflect only the mass-balanced baroclinic component of flow. Cyclical barotropic motions such as those due to tides or internal waves can, however, confuse interpretation of net motion using short-term direct current measurements. Internal wave displacements may also produce or suppress the appearance of small eddies in the baroclinic representation of flow (Knauss 1962). Local accelerations, *e.g.,* from storm activity, can cause poor estimates of flow velocity from the baroclinic representation.

Due to California Cooperative Oceanic Fisheries Investigations (CalCOFI) sample spacing (nominally a 30 to 60-km grid, at 30 to 90-day intervals), we can consistently identify baroclinic eddies larger than approximately 100 km in diameter and those persisting for more

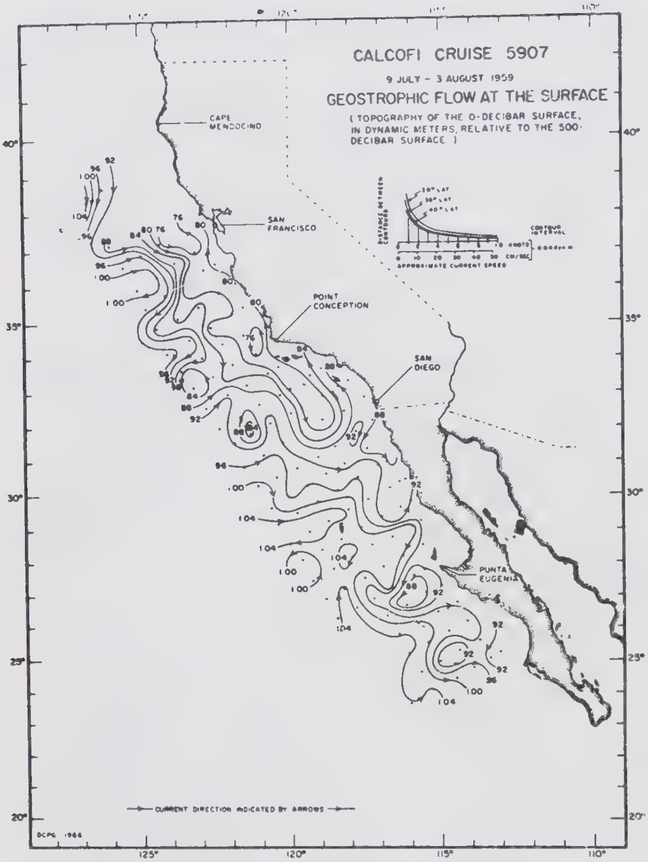

CALCOFI CRUISE 5907
9 JULY – 3 AUGUST 1959
GEOSTROPHIC FLOW AT THE SURFACE
(TOPOGRAPHY OF THE 0-DECIBAR SURFACE, IN DYNAMIC METERS, RELATIVE TO THE 500-DECIBAR SURFACE)
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
DISTANCE BETWEEN CONTOURS
20° LAT
30° LAT
40° LAT
CONTOUR INTERVAL
KNOTS
CM/SEC
APPROXIMATE CURRENT SPEED
CURRENT DIRECTION INDICATED BY ARROWS
40°
35°
30°
25°
20°
125°
120°
115°
110°

FIGURE 7. *Baroclinic representation of surface flow off the Californias in July 1959 (Wyllie 1966, p. 124). Eddies large enough to deform the density field and to be detected by the sampling grid (dots) appear as closed isobars; meanders appear as loops.*

than a month. We can resolve eddies 20 to 100 km in diameter, but at the risk of misidentifying them because of interference due to internal waves, meanders, error of measurement, and too few data points. Eddies of 20 to 100 km diameter and of less than one month's duration thus are known to exist, but their incidence and size distribution remain underestimated.

Relevant to this important range of eddy sizes is the work of Bernstein *et al.* (1977) on infrared imagery from the NOAA-3 satellite of thermal patterns in the California Current. Their work demonstrates the possibility of using thermal imagery for following eddy development and surveying their incidence, and confirms for a wide region what is observed in the field of mass and at current meter and drogue stations: most of the California Current is rich in eddies, including the flow impinging on the Channel Islands. A much more complete understanding of the distribution, persistence, and size of eddies can be anticipated from use of such satellite data to identify eddies upward of 20 km diameter and to document their genesis and decay.

Direct measurements of current speed and direction in the region off the Californias which are appropriate to eddy structure are made with difficulty and are not sufficiently numerous to support general conclusions on eddy incidence. Direct measurements made in the CCS by following parachute drogues (*e.g.*, SIO 1962) or by moored, recording current meters (*e.g.*, Lam 1972, Hendricks 1979) demonstrate flow variations consistent with effects of eddies of 10 to 50 km diameter which persist in deep and shallow waters for a few days to a few weeks. On the larger scale, baroclinic eddies from 100 to 1,000 km diameter and of months to years

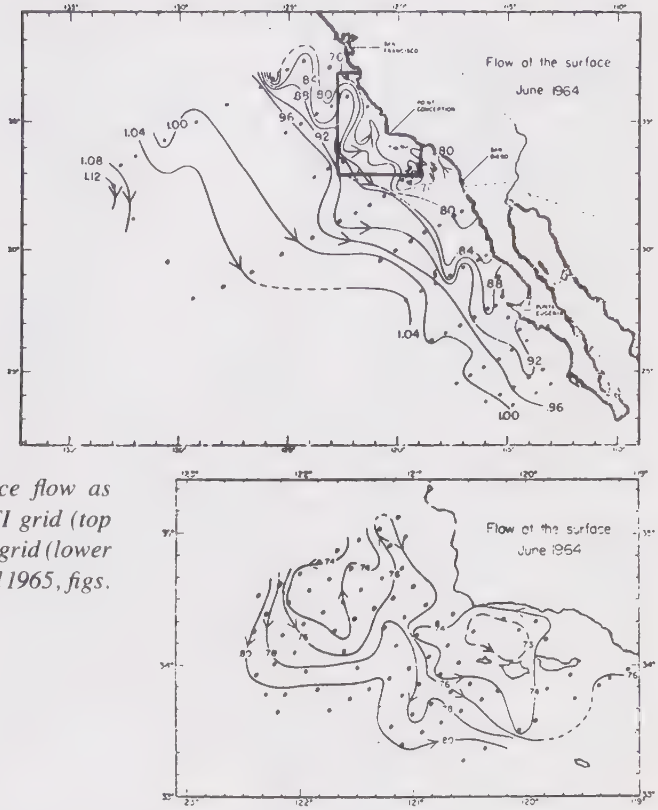


FIGURE 8. *Baroclinic surface flow as represented from the CalCOFI grid (top panel) and from an intensified grid (lower panel) in June 1964 (from Reid 1965, figs. 41, 42).*

duration are identifiable from the somewhat systematic coverage of the CCS region by surveys of the CalCOFI program. Tests of the hypothesis that flow in the CCS is balanced by the mass field have been conducted and the geostrophic method was shown to agree with various direct current measurements and to afford a somewhat better estimate of direction than of magnitude (Reid 1961, 1963, Reid and Schwartzlose 1962).

The geostrophic method also has been shown to apply in particular to eddy flow in the CCS. Baroclinic representation of an isolated eddy of about 80 km diameter was shown to agree well with drogue trajectories (Reid *et al.* 1963). This demonstrated the coherence of the velocity and mass fields and thus confirmed the adequacy of the baroclinic mode for representing eddy flow on the 100-km scale and for identifying smaller eddies, as well. Reid *et al.* (*op. cit.*) point out, perhaps as a cautionary note, that the particular eddy they describe would have "slipped through the mesh of the [CalCOFI] station grid" used for the geostrophic description had not a hydrographic station been added to the grid after discovery of the eddy by drogue work.

The incidence of baroclinic eddies and meanders in the main flow of the CCS and in the SC Bight is high. Virtually every chart of the baroclinic mode of flow given by Wyllie (1966) exhibits irregularities upstream of the island and bank system and in the CCS in general (Fig. 7). The California Current System, including flow impinging on islands, is probably rich in eddies smaller than 100 km, as well. Though some are known to be missed by the CalCOFI grid, small eddies nevertheless are often sampled and are common features in the baroclinic flow of the CCS (Wyllie 1966). Irregularities and eddies of small extent are apparent in charts of geostrophic flow off Point Conception for both January and June of 1964 (Fig. 8), periods when

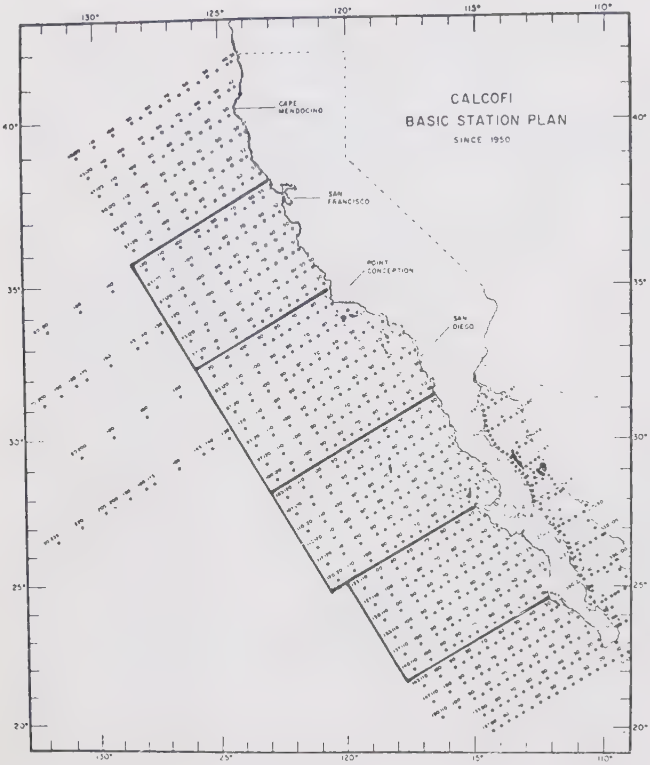


FIGURE 9. *Sectors of the CalCOFI grid used to enumerate baroclinic eddies of the California Current System. The sector containing the SC Bight covers 25 per cent more area than the others.*

the observation grid was augmented to give twice the resolution of the standard grid. As Reid (1965) notes, closer-spaced grids always seem to show proportionately smaller, but no less numerous, eddies.

Eddies in the California Current System, as defined by one or more closed streamlines of baroclinic flow, were enumerated from the charts of Wyllie (1966) by season in four size classes and four sectors off the Californias. I chose the sectors defined in Figure 9 to represent segments of the coastline between San Francisco Bay (38° N), Point Conception (35° N), Cabo Colnett (31° N), Punta Eugenia (28° N), and Bahía Magdalena (25° N). The sectors were covered, in part or totally, by 112 CalCOFI survey periods from 1949 to 1965. Separate counts were made of cyclonic and anticyclonic eddies because of their presumably different biological effects and modes of genesis. As a matter of convenience, eddy incidence is expressed as the mean number occurring in ten years, although the record used was 16 years in duration. Mean ten-year eddy incidences, corrected for gaps in coverage, are shown in Table 1. As noted above, the incidences of 20 to 100-km eddies are minimum estimates because at least some eddies of this size range were missed by the CalCOFI surveys. Larger eddies were missed when survey frequency was reduced.

Table 1 defines the level of eddy incidence in the CCS, demonstrating that eddies of all detectable sizes usually are present throughout the region off the Californias. It is also evident that there are times which show a low incidence of eddies of a given size or type. Eddy incidence demonstrates no significant seasonal variation except perhaps in the southernmost sector. Large eddies are rarer than small eddies in the Baja California sectors, but off California, eddies >200 km occur more often than those of 100 to 200 km diameter. In all areas and

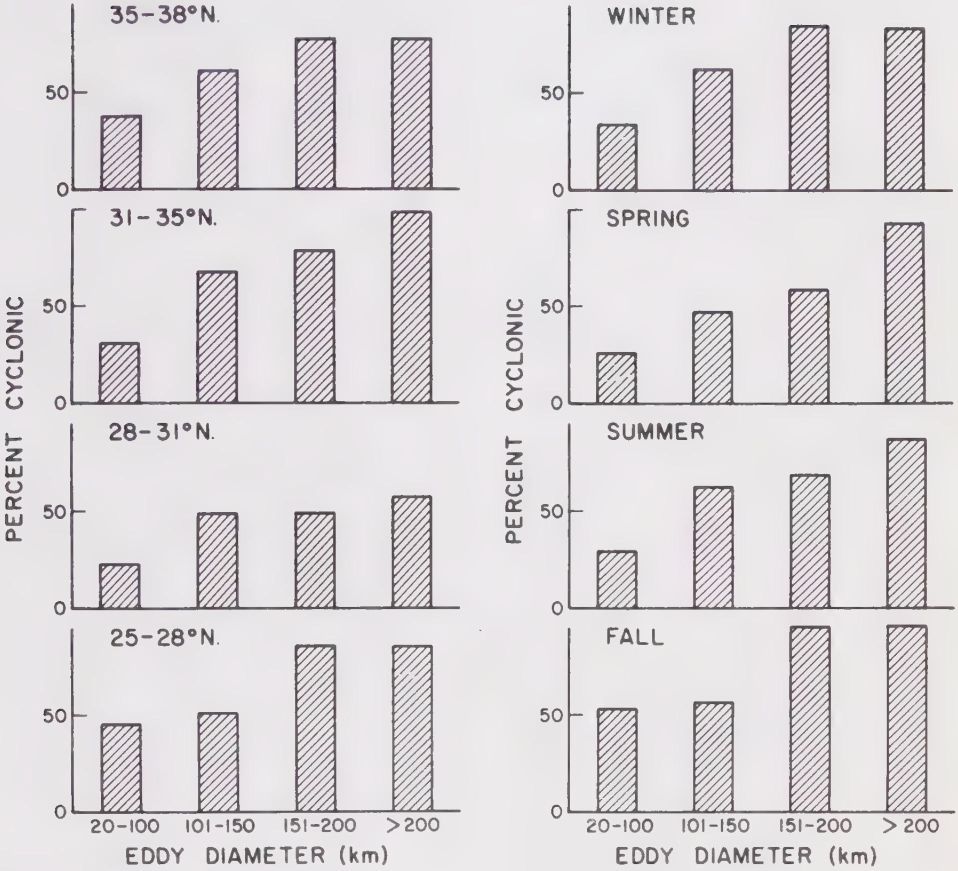


FIGURE 10. *Incidence of eddy type by size, sector, and season in the California Current System from Table 1. Panel A, by sector; Panel B, by season.*

seasons, eddies <100 km occur most frequently. In the sector containing the SC Bight, eddy incidence is dominated by the consistent (but not constant) presence of the SC Eddy. In this sector there is a corresponding paucity of both large anticyclonic eddies and small cyclonic eddies. The high incidence of small anticyclonic eddies in this sector, as well as in the two adjacent sectors, indicates that the small eddies could have been spawned by larger and more predominantly cyclonic eddies as a result of flow instabilities.

The dominance of cyclonic over anticyclonic eddies is seen in Figure 10 to occur progressively with increasing eddy size in each of the four sectors (Panel A) and in all four seasons (Panel B). The progression is most pronounced in the SC Bight (Panel A), due to the SC Eddy. This preponderance of cyclonic eddies may be ascribed to lateral friction augmented by planetary vorticity. Eddies created by lateral friction of the southward flow of the California Current against the coastal topography would be predominantly cyclonic due to inshore drag in the boundary zone. Perhaps more effective on smaller scales, the decrease in wind velocity between the coastline and the offshore maximum (discussed below) favors formation of cyclonic eddies. Wind stress gradients may be seen (charts 37 to 48 *in* Nelson 1977) to impart torque in the proper direction to favor cyclonic eddy formation in all months of the year in each

TABLE 1. Mean 10-year incidence of eddies by size, type, area, and season in the California Current System, 1949 - 1965, coast to 300 nautical miles offshore.

Eddy diameter (km)		20-100		101-150	
Eddy type*		a	c	a	c
Sector/season†					
35-38° N	Winter	0.4	0.4	0.4	1.7
	Spring	2.8	0.9	1.3	1.3
	Summer	3.6	2.3	0.9	1.9
	Fall	0.6	1.0	2.7	3.3
	Annual	7.4	4.6	5.3	8.2
	Per cent c	38.3		60.7	
31-35° N	Winter	5.0	2.0	1.0	1.1
	Spring	3.7	2.3	0.2	1.3
	Summer	6.2	1.9	0.3	1.6
	Fall	3.0	2.1	1.6	2.4
	Annual	17.9	8.3	3.1	6.4
	Per cent c	31.7		67.4	
28-31° N	Winter	2.1	0.7	0.4	0.4
	Spring	4.1	1.5	2.8	2.4
	Summer	3.1	0.6	1.4	1.7
	Fall	1.6	0.5	1.6	1.3
	Annual	10.9	3.3	6.2	5.8
	Per cent c	23.2		48.3	
25-28° N	Winter	1.1	1.4	0.7	1.0
	Spring	3.2	0	1.8	0.5
	Summer	4.0	2.2	1.8	2.1
	Fall	3.3	6.1	2.3	3.3
	Annual	11.6	9.7	6.6	6.9
	Per cent c	45.5		51.1	
All areas 25-38° N		47.8	25.9	21.2	27.3
	Per cent c	35.1		56.3	

* a = anticyclonic; c = cyclonic.

†Winter = January, February, March; spring = April, May, June; summer = July, August, September; fall = October, November, December.

151-200		>200		All sizes		Per cent c =
a	c	a	c	$\sum$ a	$\sum$ c	$100\frac{c}{a+c}$
0	1.9	2.4	3.7	3.2	7.7	
0.9	0.3	0	1.8	5.0	4.3	
0.9	0.9	0	2.0	5.4	7.0	
0	2.9	0.6	2.7	3.9	10.0	
1.8	6.0	3.0	10.2	17.5	29.0	
76.9		77.3				62.3
1.0	3.7	0	7.2	7.0	13.9	
0.9	2.6	0	6.4	4.9	12.7	
0	1.0	0.3	9.2	6.7	13.6	
0	0	0	7.3	4.6	11.9	
1.9	7.3	0.3	30.1	23.2	52.1	
79.3		99.0				69.2
1.1	0	1.5	1.2	5.1	2.3	
1.0	1.1	0.4	1.6	8.3	6.6	
2.0	2.2	1.4	0.6	7.9	5.1	
0.3	1.0	0	1.1	3.5	3.9	
4.4	4.3	3.3	4.5	24.8	17.9	
49.4		57.7				41.9
0	0.7	0.3	0.3	2.1	3.4	
0.7	0.9	0.3	0.3	6.0	1.7	
0.3	2.7	0.3	1.0	6.4	8.0	
0	2.0	0	3.8	5.6	15.2	
1.0	6.3	0.9	5.4	20.1	28.3	
86.3		85.7				58.5
9.1	23.9	7.5	50.2	85.6	127.3	
72.4		87.0				59.8

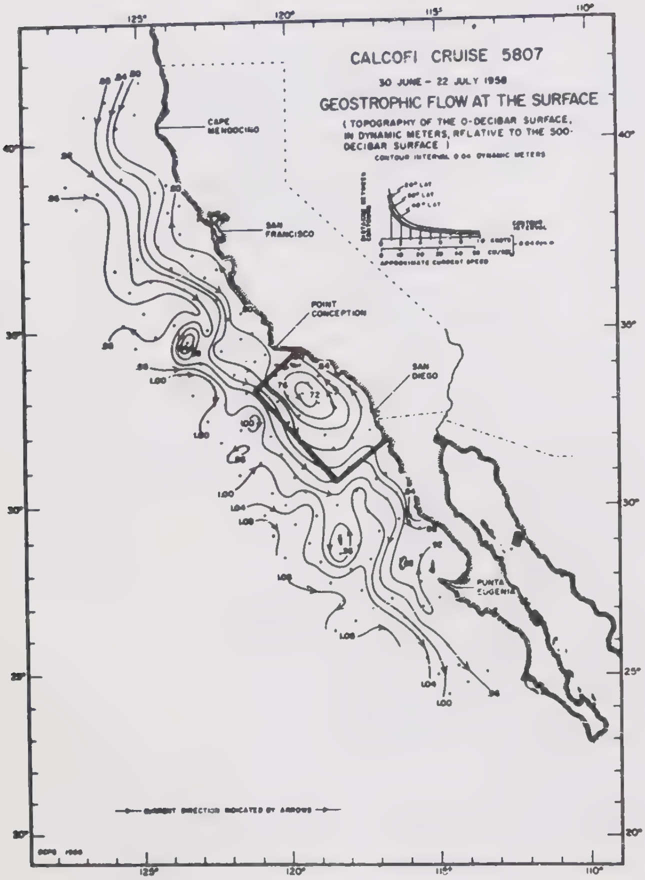

CALCOFI CRUISE 5807
30 JUNE - 22 JULY 1958
GEOSTROPHIC FLOW AT THE SURFACE
(TOPOGRAPHY OF THE 0-DECIBAR SURFACE, IN DYNAMIC METERS, RELATIVE TO THE 500-DECIBAR SURFACE)
CONTOUR INTERVAL 0.04 DYNAMIC METERS
APPROXIMATE CURRENT SPEED
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
CURRENT DIRECTION INDICATED BY ARROWS
125°
120°
115°
110°
40°
35°
30°
25°
20°
72
76
84
100

Figure 11. *Baroclinic representation of surface flow off the Californias in July 1958 (from Wyllie 1966, p. 111). The SC Eddy pattern (boxed) appears as a depression in the field of dynamic height anomaly.*

sector examined (Fig. 9), with the consistent exception of the southern half of the sector from 28° to 31° N off Baja California. This exception is important, as it helps explain the reduced incidence of cyclonic eddies in this one sector (Fig. 10, Panel A).

Finally, predominance of cyclonic over anticyclonic eddies is favored by their equatorial transport by the California Current due to conservation of angular momentum. Weak augmentation of cyclonic eddies and suppression of anticyclonic eddies occur by the Coriolis Effect (*cf.* von Arx 1962). With the exception of the SC Eddy, discussed below, the intensity (circulation strength) of eddies detected by CalCOFI surveys cannot be as well assessed as their incidence and type. This is due to the somewhat ephemeral nature of the eddies and to the inaccuracies of the geostrophic approximation of the baroclinic representation of flow. An intense eddy can thus appear weak in the charts analyzed, and *vice versa*.

SOUTHERN CALIFORNIA EDDY

The SC Eddy is the most resolvable of the eddies in the California Current System by virtue of its large scale and degree of permanence, which usually exceed the mesh and frequency of CalCOFI grid observations. Examples of eddies at least as large and intense as the SC Eddy are found in the main flow of the California Current (*e.g.*, Wyllie 1966), but have not been measured in further detail because of their transitory character.

One of the better examples given by Wyllie (1966) from the CalCOFI data is shown in Figure

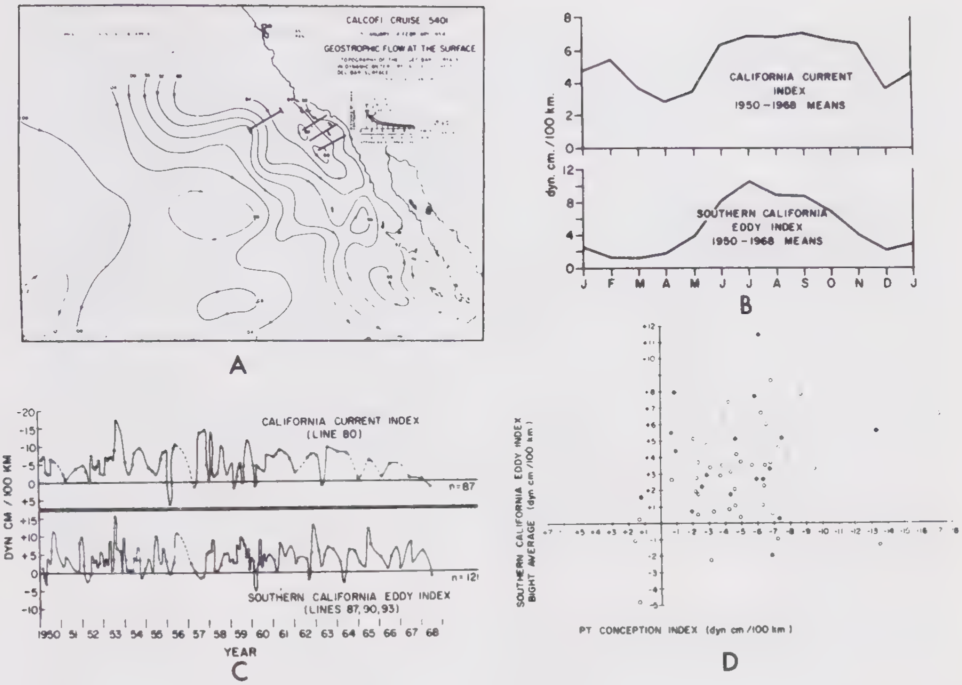


FIGURE 12. *Indices of baroclinic flow across sections (Panel A) off Point Conception (Panel B and C upper) and in the SC Eddy (Panel B and C lower), and the relationship between individual index pairs (Panel D). Indices derived from Wyllie (1966) by the author.*

11. The pattern of the SC Eddy (boxed) was augmented by the surfaced coastal countercurrent in this period (July 1958). Offshore, the eddy was augmented by a southwest-flowing, jet-like intensification of the California Current, which appears to have spawned two offshore eddies (one 200 km west of Point Conception and one centered near Guadalupe Island).

The SC Eddy, from Wyllie (1966) and Figure 12, Panel C, was present in every year (1949 to 1964) from July through January. From February through May, the time of the spring phytoplankton boom and the spawning of the northern anchovy (*Engraulis mordax*), the SC Eddy may periodically disappear for a month or more, flushing the surface waters of the SC Bight. Flushing is episodic in character, but most frequent in April (3 of 13 cases). The eddy may also "dissolve" in the baroclinic representation to an indeterminate field of weak flow. Such dissolution occurs in the same season as does flushing (again, 3 of 13 cases are in April). The eddy usually persists, however, in the absence of the surface countercurrent. This typically occurs in April to May, a period when the intensified California Current overrides the coastal countercurrent, to paraphrase Wyllie (1966). This pattern of events is supported by independent conclusions from drift bottle release and return statistics (Schwartzlose 1962, Squire 1977), and by the intensity of the SC Eddy, as I will now discuss.

The SC Eddy affords the best conditions for estimating changes in eddy flow intensity. Its stationary location and usual large size permit use of CalCOFI survey measurements to characterize two aspects of its flow: southward impinging flow off Point Conception, and the return flow of the inshore limb of the eddy. I computed indices of circulation strength from CalCOFI cruise measurements of the baroclinic slope of the sea surface (0/500 db; Wyllie 1966) across sections defined in Figure 12, Panel A. I chose these sections to show variations of strength of the California Current off Point Conception (northernmost section) and of the inshore limb of the SC Eddy and SC Countercurrent, when present (mean value of seaward slope across the three lower sections). Slopes shoreward of the index sections were not included in the eddy slope means to avoid effects of boundary instabilities associated with upwelling, nor were those off Point Conception to avoid including as well the effect of the Davidson Current, when present. The average annual cycle of flow past Point Conception in the period 1950 to 1968 (Fig. 12, Panel B, upper) is seen to be regular and to agree with the cycle and magnitude of circulation of the SC Eddy (Panel B, lower), which might be expected if the impinging flow drives the eddy, as noted by Pavlova (1966). The seasonal cycle of average surface flow impinging on the SC Bight (Panel B, upper) is in essential agreement with results of Reid (1965); offshore southward flow occurs all year off Point Conception and is strongest from May through November and weakest in spring. Circulation strength of the SC Eddy, as measured by flow of its inshore limb, is seen in Panel B to be greatest from June through October and least from December through April. Reid (1965) notes that the eddy's inshore limb develops to such a degree that it rounds Point Conception from October through January, and then constitutes a coastal countercurrent. He also shows that the Northern Channel Islands usually experience seasonal reversals of current direction due to their inclusion in the eddy's inshore limb from July through February.

Examination of flow across these sections month by month and year by year adds a perspective of the effects of eddies and meanders on flow estimation and indicates a high frequency of eddies imbedded in the mean flow to and through the Channel Island system. The time sequence of individual flow estimates, shown in Panel C of Figure 12, reveals a degree of variation in both incident and eddy flow intensity which is not apparent in the plots of averaged flow values of Panel B. This is because transient baroclinic-scale eddies and meanders detected in the flow are suppressed upon averaging. The fluctuations of individual indices in Panel C are caused by perturbations large enough to affect the field of mass, since the flow estimates were derived from the distribution of mass. Eddies or meanders of less than about 10 km radius (of curvature) or 5 days duration are unlikely to produce a detectable change in the mass field. The plots of Figure 12, therefore, reflect the abundance of eddies exceeding these dimensions.

Owing in part to the effects of eddies and meanders *not* reflected in the indices, it is difficult to predict flow intensity at a particular time and to specify the particular response of the SC Eddy to changes in impinging flow intensity. This is shown by the scatter of data points in Panel D of Figure 12.

PACIFIC EDDY COMPARISONS

It is of interest to compare SC Eddy characteristics with those of large eddies elsewhere in the Pacific, some of which have been investigated more intensively. A documented example of baroclinic doming and upwelling is provided by the Costa Rica Dome, produced by a major northward deflection of the North Equatorial Countercurrent as it impinges on the American continent (Wyrtki 1964). The dome is located in the bight of this deflection in a region where nutrients and thermocline both are close to the photic depth (Brandhorst 1958, Thomas 1970, Owen and Zeitzschel 1970a). Its physical characteristics denote a stationary, cyclonic eddy large enough to demonstrate nutrient enrichment effects (Brandhorst 1958, Broenkow 1965, Thomas 1970, 1977) and the responses of phytoplankton, zooplankton, and small nekton stocks (Blackburn *et al.* 1970, Owen and Zeitzschel 1970b, and references above).

A contrasting case is provided by the Hawaii Eddy phenomenon described previously. Despite the large vertical displacement (50 to 150 m) of the thermocline that is attributable to doming by the eddy (Patzert 1970), nutrient-rich waters lie deep. For enrichment of the photic zone to occur, water deeper than about 300 m would have to be raised more than 200 m to reach the bottom of the photic zone. McGary (1955) consequently found no evidence for photic zone enrichment that could be attributed to the Hawaii Eddy. Other significant biological processes are, however, evidently affected by the Hawaii Eddy; Sette (1955) describes evidence for the effect of the eddy on local fish populations.

Uda and Ishino (1958) have identified patterns of enrichment resulting from eddy systems off Japan comparable in scale and persistence to those off the Californias and Costa Rica. Areas of high concentrations of commercially and ecologically important fish, squid, whales, plankton, and benthic fauna were found to coincide with areas of high eddy activity, both near and far from land boundaries. Uda and Ishino distinguished between topographical eddy systems (those affected by topography) and dynamic eddy systems (those affected by current "collision").

Table 2 gives estimated magnitudes of various properties of the SC Eddy, together with reported magnitudes of California coastal upwelling and of other large eddy systems in the Pacific. As may be seen in the geostrophic flow atlas (Wyllie 1966), the SC Eddy may deviate from Table 2 values of size and circulation strength. This is caused in part by change in the obstacle profile confronting the current when changes occur in either the direction or depth span of the impinging flow.

Several comparisons of magnitude estimates in Table 2 are worth comment. Despite the varying eddy sizes, intensities, and vertical velocities, transport by upwelling is of the same order of magnitude in the SC Eddy, Hawaii Eddy, Costa Rica Dome, and in a segment of the coastal upwelling domain 200 km in length (the same distance along the California coast usually subtended by the SC Eddy). As may be seen from ambient nutricline and photic depths, nutrients are readily available for transfer up through the photic zone in all areas considered, except off Hawaii. The degree of enrichment and subsequent productivity of the SC Eddy is probably comparable, therefore, to that of other major eddy systems. The SC Eddy appears only slightly less effective in total transport of nutrients into the photic zone than does upwelling along a comparable length of the California coastline, although SC Eddy nutrients are transported into about three times the volume. Such ecological impact is enhanced by the role of the SC Eddy as an oceanic reservoir for washout of coastal and upwelling products from the Southern California Bight, as well as from Point Conception and farther north.

ECOLOGICAL EFFECTS OF THE SOUTHERN CALIFORNIA EDDY

Several biological effects of the SC Eddy have been identified in studies of phytoplankton concentrations and communities, zooplankton, and fish populations. Allen (1945) examined vernal distribution of diatom populations and abundances in the upper 60 m over the SC Bight in relation to baroclinic flow and bathymetry. The area of the Santa Rosa-Cortez Ridge system above 200 m depth is treated as an obstacle. Allen indicates local topographic control of both current patterns and of diatom abundance on a relatively intensified sampling grid (25-km spacing, six cruises in three months). He presents spatial variations of diatom concentrations ranging over five orders of magnitude in patterns which support his hypothesis that higher diatom concentrations occur off the Santa Rosa-Cortez Ridge axis, partly due to washdown of coastal upwelling from the north. The ridge axis usually defines that of the SC Eddy.

Sargent and Walker (1948), from a similar data set, examined patterns of abundance of several diatom populations sampled in the upper 60 m in and beyond the SC Bight. They considered these populations to be closely associated with what they treated as "cyclonic eddies of freshly upwelled water entering the area of observation from the north" (off Point Conception), which appear identical in size and persistence to the SC Eddy. Greater abundance of

TABLE 2. Parameters of Pacific eddies and California coastal upwelling.

	Southern California Eddy[1]	Johnson Atoll[2]	Hawaii Eddy[3]	Costa Rica Dome[4]	Small CCS Eddy[5]	California coastal upwelling[6]
Obstacle diameter (km)	200	26	100 (wind) 300 (current)	—	—	200 (length†)
Eddy type	stationary, topographic-dynamic	vortex street	wind-forced	free, stationary	free, stationary	(edge eddies)
Ambient* or incident flow (cm/sec)	20	60	30	55	20	20
Eddy flow (cm/sec) at 1/2 radius	30	80	50	40	20	—
Radius (km)	100	30	65	200	40	—
Decay time (days to 1/e)	100	16	>65	—	>14	14
Vertical velocity (m/day)	0.3	—	0.8 (initial)	0.1	—	1.0
Upwelling volume (m^3/day)	10^{10}	—	10^{10}	10^{10}	—	10^{10}†
Pycnocline elevation $\left(\frac{\text{ambient-dome}}{\text{ambient}}\right)$	0.3-0.5	—	0.4	0.7	0.1	0.4-0.6
Ambient* photic depth (m)	60	100	100	70	70	60
Ambient* nutricline depth (m)	30-70	75	300	40	40	20-60

Sources: [1] McEwen 1948; Wyllie 1966; Wyllie and Lynn 1971; Owen 1974.
[2] Barkley 1972; Frederick 1970.
[3] Patzert 1970; McGary 1955; Frederick 1970.
[4] Wyrtki 1964; Broenkow 1965; Bennett 1963; Owen and Zeitzschel 1970a.
[5] Reid *et al.* 1963; Owen and Sanchez 1974.
[6] Bakun 1973; Walsh *et al.* 1974; McEwen 1948; Wyllie and Lynn 1971; Arthur 1965; Sverdrup and Fleming 1941; Owen and Sanchez 1974.

* "Ambient" refers to condition in absence of phenomenon.
† 200-km coastal strip 50 km wide for comparison with SC Eddy.

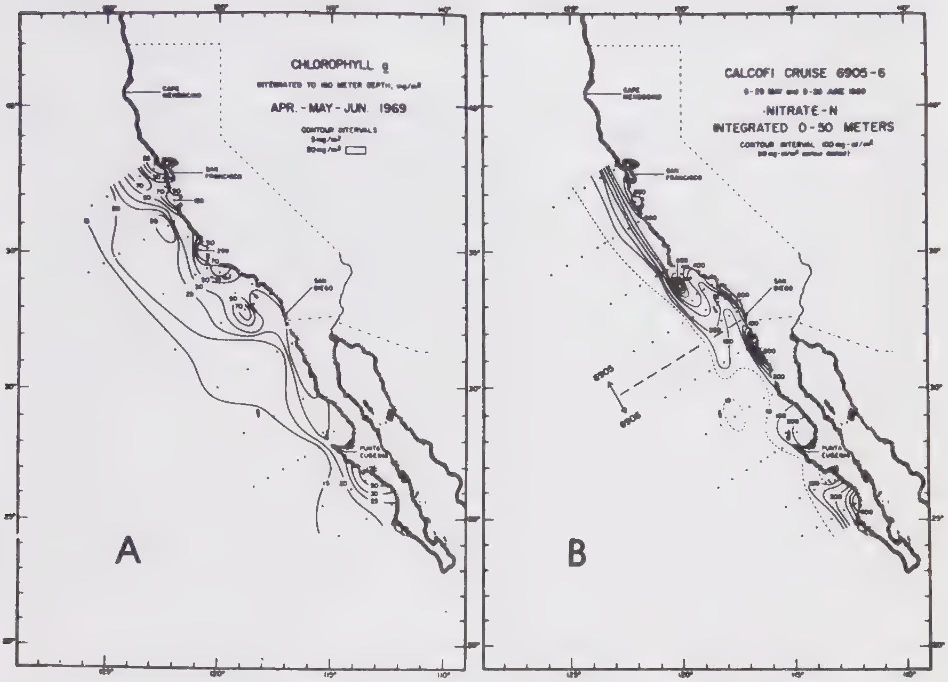


FIGURE 13. *Total chlorophyll* a *(mg/m²) to 150 m depth (Panel A, Owen 1974, p. 107) and total nitrate-nitrogen to 50 m depth (Panel B, Thomas and Seibert 1974, p. 37) off the Californias in spring 1969.*

several diatom populations in the offshore limb of the eddy was attributed to entraining of upwelled water north of Point Conception. Diminished abundances in the inshore limb were ascribed to nutrient depletion and grazing as the phytoplankton circuited the eddy. Change in phytoplankton community composition was also detected as the populations circuited the eddy, consistent with Allen's (1945) distinction between diatom communities inshore and seaward of the Santa Rosa-Cortez Ridge.

Spatial variation of community structure and of population densities is enhanced by the SC Eddy. Succession of community composition occurs along flow streamlines; where such streamlines are closed, as in the SC Eddy, successive communities are inevitably juxtaposed. This is apparent from the work cited above, which suggests a change in time and space from a diatom species ensemble characteristic of recent coastal upwelling to an ensemble characteristic of older surface-layer waters. Due to the SC Eddy, these ensembles were spatially juxtaposed in what may prove to be a characteristic state. This state demonstrates (perhaps more crudely than actually occurs) the creation of community patchiness by stirring, as defined by Eckart (1948), and is not necessarily confined to the phytoplankton alone.

Patterns of high phytoplankton concentration which correspond to those of the SC Eddy are shown by Owen (1974) and by Owen and Sanchez (1974) in terms of surface and depth-integrated chlorophyll *a* concentrations (Fig. 13, Panel A). These corresponded with patterns of surface-layer nutrient distribution of Thomas and Seibert (1974) at times when the SC Eddy was fully developed (Panel B). Together with the evidence for high persistence of the SC Eddy, these studies confirm that the effects observed by Allen and by Sargent and Walker are characteristic (rather than episodic) in the SC Bight. Primary production measurements in the SC Bight are too sparse to demonstrate an enrichment effect of the SC Eddy. A single transect of such measurements across the SC Bight (Owen 1974) showed primary production to be about six times greater in the SC Eddy than beyond it.

Brinton (1976) studied the population biology of *Euphausia pacifica,* the dominant species among the larger zooplankton of the SC Bight. He identified the SC Eddy and its associated upwelling regimes as a productive refuge for an identifiable population of the species.

Benthic-dwelling organisms with planktonic life history stages (usually larval) depend for population maintenance on being deposited, at the end of their planktonic stage, in waters shoal enough to permit their survival on the sea bottom. Off the Californias, where flow frequently diverges from the coast, such populations must depend on eddies and meanders in the mean flow to return a sufficient number of their meroplankton to the habitat. Although the SC Eddy is not cited in particular, examples include populations of the spiny lobster, *Panulirus interruptus* (Johnson 1960), and the red crab, *Pleuroncodes planipes* (Longhurst 1968). Both organisms spend extended periods as plankton in their early life history.

During spawning in the 1941 season, a population of the now decimated California sardine (*Sardinops caerulea*) was shown from plankton surveys (Sette and Ahlstrom 1948) to have concentrated its eggs and larvae in an area corresponding closely to that of the SC Eddy and its elevated diatom densities (Sargent and Walker 1948). Figure 14 shows this striking local correspondence, which suggests the possible sensitivity of the sardine stock to the SC Eddy. The surveys did not cover the entire range of spawning, however, and it is possible that other eddies beyond the SC Bight may have supported undetected spawning areas.

Since the replacement of the California sardine stocks by those of the northern anchovy (*Engraulis mordax*), CalCOFI plankton surveys have covered the spawning time and area of the anchovy. These have revealed (Smith 1978) that the region inclusive of the SC Eddy, comprising about 12 per cent of the spawning area of the anchovy's central subpopulation, contained, on the average, 48 per cent of the spawned larvae during the period 1951 to 1975; since 1966 this region has contained 64 per cent.

Berner (1959), in his study of food of anchovy larvae, noted that areas where larvae were found to be actively feeding corresponded to those of the copepod nauplii maximum, as described by D. K. Arthur (1956). Comparison of areas of active larval feeding in the SC Bight with corresponding charts of baroclinic flow (Wyllie 1966) shows that the area of feeding larvae corresponded with the inshore limb of the SC Eddy, although D.K. Arthur (1977) subsequently showed that the copepod nauplii maximum may also lie on the SC Eddy axis or in its offshore limb.

SUMMARY

Owing to the rapid attenuation of sunlight with water depth, over half of the total primary production of food in the offshore CCS occurs in the surface mixed layer, 10 to 60 m deep. The primary supply of inorganic nutrients to the mixed layer is from below. Lateral transport in the mixed layer imports virtually no inorganic nutrients, except directly from coastal upwelling zones, because the phytoplankton communities of the northeastern Pacific can strip the mixed layer of extant nutrients in only a few days. Local regeneration of nutrients from mixed-layer organics is known to be a nutrient source for sustaining phytoplankton growth under otherwise impoverished conditions, but has not been proposed to sustain the higher levels of production characteristic of the CCS off California. Southward transport of the California Current imports nutrients at depth and, at the same time, creates the shoreward upslope of the thermocline layer that makes possible enrichment of the mixed layer and photic zone. Actual transfer of nutrients

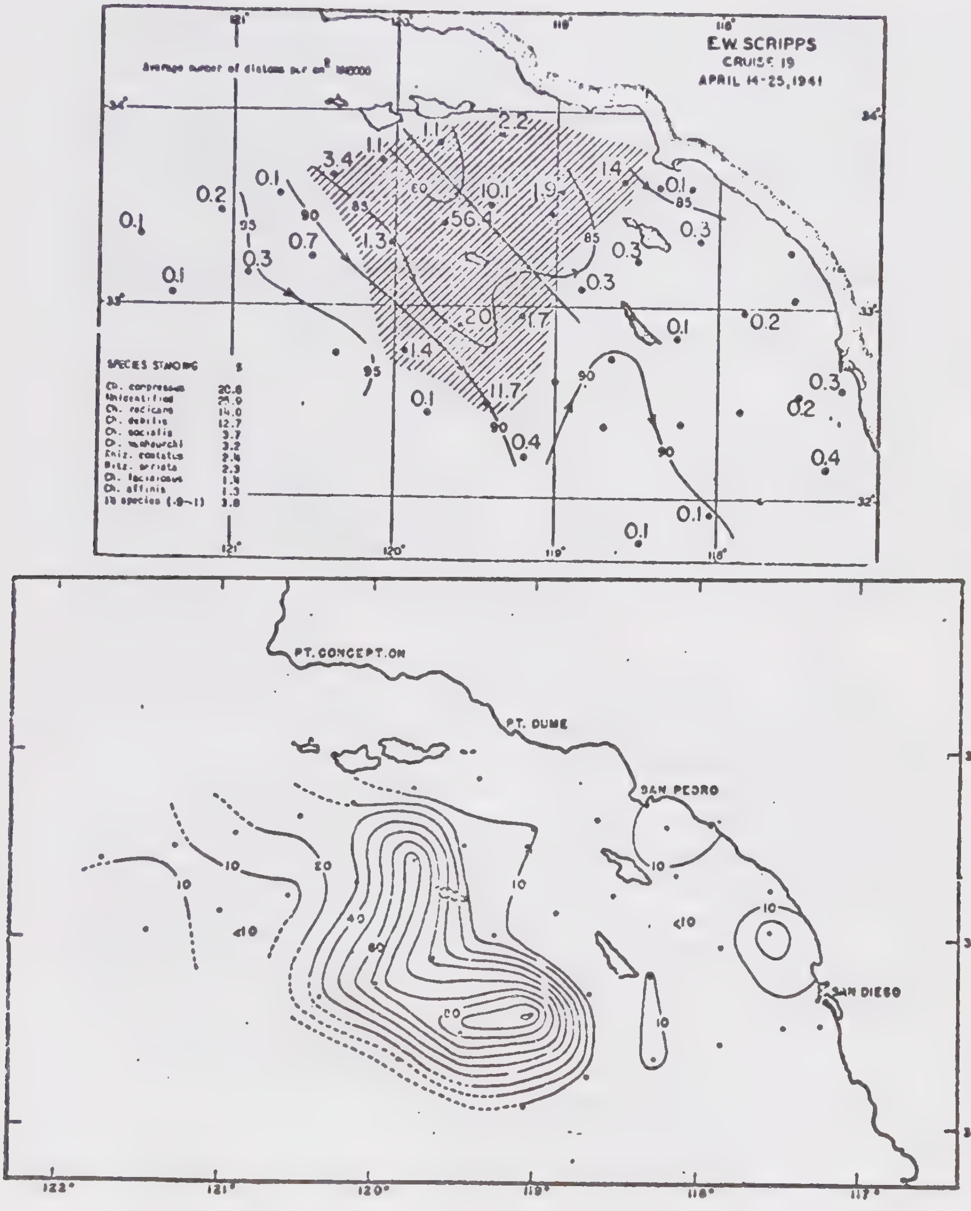

E.W. SCRIPPS
CRUISE 19
APRIL 14-25, 1941
121°
120°
119°
118°
34°
33°
32°
SPECIES STANDING
Ch. compressus 20.8
Unidentified
Ch. radicans 14.0
Ch. debilis 12.7
Ch. socialis 3.7
Ch. affinis 1.3
56.4
20
11.7
10.1
3.4
2.2
1.9
1.7
1.4
1.3
1.1
0.7
0.4
0.3
0.2
0.1
PT. CONCEPTION
PT. DUME
SAN PEDRO
SAN DIEGO
122°
121°
120°
119°
118°
117°
34°
33°
32°
10
20
40
60
80
<10

FIGURE 14. (**top**) *Distribution of diatoms and baroclinic flow in April 1941. Hatching denotes area of higher diatom abundance. Per cent contribution to total diatoms given beside each sampling location (Sargent and Walker 1948, fig. 1).* (**bottom**) *Distribution and concentration of sardine eggs over the spring 1941 spawning season. Values on isopleths are number of eggs under 10 m² of sea surface (Sette and Ahlstrom 1948, fig. 4).*

to the mixed layer at high rates is episodic. The best known episodic fertilization process is wind-driven coastal upwelling; direct effects of strong upwelling are detectable to 50 km offshore, farther off capes, and perhaps farther yet if edge-eddies transport large, cold volumes offshore. The upward transport of nutrients in the SC Eddy can evidently approach that of the coastal upwelling strip. Although injected into a larger volume of water than in coastal upwelling, nutrient enrichment by the SC Eddy is continuous rather than episodic since the SC Eddy is a persistent feature of the region. Eddies of comparable enrichment potential are usually present elsewhere in the CCS, and small eddies are commonplace. Due to their transitory nature, they are difficult to study and their ecological impacts are thus undocumented. The cyclonic eddies of the CCS nevertheless are likely to be an important and variable determinant of the standing stocks, productivity, and community structure of life in the CCS, and particularly in the SC Bight.

ACKNOWLEDGMENTS

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PATTERNING OF FLOW AND ORGANISMS IN THE LARVAL ANCHOVY ENVIRONMENT

by

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INTRODUCTION

This work reviews patterning of plankton populations and communities by their interaction with physical processes, with special reference to eastern boundary regions and their capacity to support early stages of engraulid fish populations. It describes patterning mechanisms and effects documented by case studies appropriate to a large range of scales and restates some old hypotheses. Coastal upwelling and its biological effects are treated in only a general way. The literature is extensive and is covered elsewhere in this volume (cf Bakun and Parrish).

By the time its yolk-sac is gone, an anchovy larva is a seeing animal with a functioning digestive system and an immediate need for food. It feeds by the hunt-and-peck tactic (Hunter, in press), selecting at first for rather specific particle types from the wide variety of organisms and detritus that it encounters. Favoured food particles are single, rounded plant cells or animals 20-120 mm in width which lack long spines (Arthur, 1976; de Mendiola, 1974). On the average, even in upwelling zones, it is unlikely to encounter enough particles to meet its metabolic needs (e.g., Lasker, *et al.*, 1970). This average, however, is known from methods that sample inappropriate volumes of water at inappropriate intervals. The interval immediately appropriate to a larva is the volume it searches in a day, and the path it takes to search this volume. These are as small as a litre and a few metres, respectively, as derived from Hunter's (1972) laboratory experiments, Smith's (1978) observations on plankton variability, and Vlymen's (1977) theoretical treatment of food concentration geometry and larval fish energetics. It is evident from work on inappropriately large intervals that larval food must occur in patterns in space and time to exceed concentrations larvae require, and that systematic approaches need to be taken to estimate the scale and degree of food patterning in the larval habitat in areas and at times of spawning if fishery models are to be realistically expected to specify recruitment under any particular measurable regime.

There is a considerable body of evidence that patchiness of plankton frequently and widely arises from patterned circulation. Environmental circumstances under which such patterns arise are often rather unexceptional, and thus may be more widespread than isolated case studies describe. There is also some promise of prediction of patterning and depatterning circulations, which would be of inestimable value in forecasting yield of fish stocks as affected by patterning of their food supply. Accounting for patterning of organisms should also enhance the accuracy of biological production models constructed for populations at any position in the food web.

MESOSCALE PLANKTON PATTERNING AND OFFSHORE ENRICHMENT BY EDDIES

Eddies arise from flow instability, uneven wind forcing and current deflection or separation at boundaries. They may be imbedded in the surrounding flow ("free"), or geographically stationary ("trapped"). Both free and trapped eddies can arise from frictional interaction with obstacles such as coastlines, islands and banks.

Planktonic communities, as well as some benthic and terrestrial populations, can be extended by eddy processes into otherwise marginal habitats, either continuously or ephemerally. The fate and dilution rate of anthropogenic products (e.g. MacGregor, 1974) and their effect on island, coastal and oceanic populations are also in part determined by eddy-like perturbations. Eddies also affect such local environmental conditions as temperature and nutrient distribution in the water and cloud cover in the atmosphere. Genesis, maintenance and lysis of eddies are of particular interest because organisms and substances in transit become differently distributed in space and time within and between eddies; concentrations of organisms and substances are locally maintained at higher levels and for longer periods, their trajectories are markedly different, and plankton populations which would not otherwise interact are juxtaposed. Eddies greatly amplify rates of transfer of materials (and energy) between nearshore upwelling zones characteristic of eastern boundary margins and pelagic regions well seaward of the continental shelf. Fronts that frequently bound upwelling zones cause slow subduction of surface waters into deeper, vertically stable strata of the offshore pycnocline. Eddy motion, whether the small-scale result of flow instability along the front or of mesoscale impingement from offshore, produces both surface and subsurface transport from upwelling zones.

Satellite imagery of thermal patterns at the sea surface off California indicate extensive seaward transport of cold water from upwelling zones by eddy motion. Thermal plumes can be traced for several hundred km offshore across the mean flow of the California Current (Bernstein *et al.*, 1977).

Cyclonic eddies larger than 10 km in diameters and a week's duration may have a major role in sustaining the higher biological concentrations and productivity which are characteristic of the inshore 200 km of the California Current System (CCS). Baroclinic eddies deform the density field. A cyclonic eddy or meander of sufficient size and intensity exhibits a detectable dome in surfaces of constant density to the depth where the eddy motion vanishes. Doming signals that the thermocline layer, which marks a sharp increase in water density with depth, has risen and displaced surface mixed-layer water. The displaced water is usually stripped of nutrients and often poor in phytoplankton as well. In eastern boundary regions, the thermocline is nutrient-laden and comparatively close to the sea surface. Elevation of the thermocline due to cyclonic motion thus results in upward flux of nutrients into the photic zone, which supports growth of phytoplankton. The new availability of nutrients is sustained by upwelling (here meaning upward flow across density surfaces) in and near the eddy centre and can be augmented by mixing and entrainment due to shear flow across the thermocline layer of the eddy. Additional nutrients are supplied in episodic fashion during storm activity which is either long or severe enough to erode the dome, with its relatively exposed pâte (e.g. Blackburn, 1966).

The presence of a cyclonic eddy, however, does not assure photic layer enrichment. Such a case is provided by the transitory Hawaii Eddy phenomenon. Despite the large vertical displacement (50-150 m) of the thermocline attributable to doming (Patzert, 1969), nutrient-rich waters lie too deep for enrichment of the photic zone to occur. Water deeper than about 300 m would have to be raised more than 200 m to reach the bottom of the photic zone. McGary (1955) consequently found no evidence for photic zone enrichment that could be attributed to the Hawaii eddies. Other significant biological processes are, however, evidently affected; Sette (1955) describes evidence for the effect of the eddies on local fish populations.

If an eddy is stationary, e.g. topographically trapped, it can collect and locally conserve substances washed down from the boundary layer of the obstacle(s). Small eddies with short transit times thus extend the effective area of the boundary layer. Laboratory and field work with natural phytoplankton communities (recently, Thomas *et al.*, 1980; Estrada and Blasco, 1970) indicates that phytoplankton populations respond differentially to changes in nutrient flux and can create new sequences of community position on time scales greater than a few days. Transit times around mesoscale eddies are longer, so that new and distinguishable community compositions may arise at higher trophic levels as well as at the level of primary production. Thus seed populations in large trapped eddies can respond differentially and rapidly create new community sequences in transit. Close examination of biological effects of eddies seems warranted, for example, to determine whether eddy processes affect production of food organisms that support larvae and adults of the commercially and ecologically significant anchovy, *Engraulis mordax*. This may occur through effects of eddies on boundary layer extension, community structure, productivity and concentration of small plankton; all important factors in determining survival of the large numbers of anchovy spawned in such regions (Lasker, 1975; Smith, 1978).

Eddy genesis

In the vicinity of the island, bank and coastline systems, combinations of wind, current and topographic effects must be invoked to explain patterns of circulation (Pavlova, 1966; Arthur, 1965; Reid, 1965). The variability of flow impinging on obstacles couples with local topography to create or suppress eddy and front patterns. Wind patterns exercise significant control upstream by determining the impinging flow intensity and direction, and locally by augmenting or cancelling the topographic perturbations of water flow. Local-scale wind patterns are in turn affected by islands and coastlines. It is easy to understand why no theoretical treatment of flow consistently accounts for observed current patterns downstream of the islands, banks and coastlines of eastern ocean boundaries.

Large-scale eddy genesis by wind is indicated in Nelson's (1977) water transport calculations, derived from wind patterns off the west coast of North America. Flow directions are shown which are consistent with equatorward transport of the California Current, onshore transport south of the Southern California Bight, and nearshore poleward transport of the Southern California Countercurrent. These are elements of the Southern California Eddy, although Nelson's averaging scale is too large to resolve this eddy directly. On smaller scales, case studies (e.g. SIO 1962; Patzert, 1970) have shown that uneven wind distributions can create eddy circulations.

The distribution of wind speed and direction over the region of the Southern California Bight during northwest wind conditions (U.S. Dept. of Interior, 1978) may exhibit a two-jet system, consistent with wind retardation by the northern Channel Islands of a single jet impinging from the north. A high-wind zone is characteristic about 200 km off the California coast from April through August (Reid *et al.*, 1958; Alan Hancock Foundation, 1965). Its role in eddy genesis is unassessed as yet, although jet-like winds impart stress transport that would favour formation of small-scale mesoscale eddies.

Reports of atmospheric and oceanic eddy systems due to islands often taking the appearance of von Kārmān vortex wakes, have become well documented in recent years. Barkley's (1972) oceanographic study of Johnston Atoll's wake is the definitive example of vortex shedding of water by an island. As Barkley states, increasing reports of atmospheric marine effects are due to "... a special combination of circumstances: the wind, an obstacle, the right kind and quantity of cloud cover at the proper level, and a satellite overhead taking pictures; all must be present." Vortex wakes and other types of eddy patterns due to boundaries are apt to be common in ocean and atmosphere. Berger and Willie (1972) and Chopra (1973) review these phenomena and their dynamics. Of obstacles in the CCS, only Isla Guadalupe receives direct mention, but Chopra also reports effects of both smaller and larger islands elsewhere which show that obstacles of virtually any size may produce systematic flow deviations. Boundaries and direct wind effects are not prerequisities for eddy formation. Instability of flow can develop from current jets and convergences (e.g. Barkley, 1968) and eddies are commonplace in the open sea (Bernstein & White 1974). Uda and Ishino (1958) have identified patterns of enrichment resulting from free eddy systems off Japan. The eddies are comparable in scale to those off the Californias and Costa Rica. Areas of high concentrations of commercially and ecologically important fish, squid, whales, plankton and benthic fauna were found to coincide with areas of high eddy activity, both near to and far from land boundaries. Uda and Ishino distinguished between topographical and dynamic eddy systems and identified eddies affected both by topography and current collision (dynamic). Detection of eddies and their formation, persistence and decay by satellite sensing of sea temperature patterns shows particular promise (Bernstein *et al.*, 1977), although stratus clouds frequently obscure the sea surface in eastern boundary regions. Even in cloud-free periods, atmospheric path absorption effects need to be subtracted from sea-surface radiance patterns before satellite studies of eddies can proceed beyond qualitative detection.

Baroclinic eddy incidence and size

The geostrophic method has been shown to apply in particular to representing eddy flow at mid-latitudes. Baroclinic representation of an isolated eddy of about 80 km diameter in the CCS corresponded well with drogue trajectories (Reid *et al.*, 1963). This study demonstrated coherence of the velocity and mass fields and so confirmed the adequacy of the baroclinic mode for representing eddy flow on the mesoscale and for identifying smaller eddies as well. Reid *et al.* pointed out, perhaps as a cautionary note, that the particular eddy they described would have "slipped through the mesh of the /‾CalCOFI_7 station grid" used for geostrophic description if it were not for a hydrographic station added to the grid in response to the discovery of the eddy by drogue work. This illustrates the general limitations of eddy detection by the geostrophic method, as ship surveys cannot be conducted continuously, nor sample all appropriate scales.

Eddies in the California Current System, as defined by one or more closed streamlines of baroclinic flow, have been enumerated from the charts of Wyllie (1966) by season in four size classes and four sectors off the Californias. I chose the sectors to represent segments of roughly equal area off the coastline between San Francisco Bay (38° N), Pt. Conception (35° N), Cabo Colnett (31° N), Pta. Eugenia (28° N) and Bahia Magdalena (25° N). The sectors were covered, in part or totally, by 112 CalCOFI survey periods from 1949-1965. Separate counts were made of cyclonic and anticyclonic eddies because of their presumably different biological effects and modes of genesis. As a matter of convenience, eddy incidence is expressed as the mean number occurring in ten years although the record used was 16 years in duration. Mean ten-year eddy incidences, corrected for gaps in coverage, are shown in Table 1 (from Owen, 1980). The estimations of incidence of 20-100 km eddies are the least accurate because some eddies of this size range obviously were missed by the CalCOFI survey timing and grid and because interval waves can create images of small eddies. Larger eddies also were missed when survey frequency was reduced.

Table 1 summarizes eddy incidence in four regions of the CCS and shows that eddies of all sizes detectable from the CalCOFI grid usually are present throughout the region off the Californias. Eddy incidence demonstrated no obvious seasonal variation except perhaps in the southernmost sector. Large eddies are rarer than small eddies in the Baja California sectors, but off California eddies larger than 200 km occur more often than those of 100-200 km diameter. In all areas and seasons, eddies smaller than 100 km occur most frequently. In the sector containing the Southern California Bight, eddy incidence is dominated by the consistent (but not constant) presence of the Southern California Eddy. In this sector there is a corresponding paucity both of large anticyclonic eddies and of small cyclonic eddies. The high incidence of small anticyclonic eddies in this sector, as well as of the two adjacent sectors, indicates that the small eddies could have derived from larger and predominantly cyclonic eddies, perhaps as a result of flow instabilities. The dominance of cyclonic over anticyclonic eddies is seen in Table 1 to occur progressively with increasing eddy size in each of the four sectors and in all four seasons.

Table 1. Mean 10-year incidence of eddies by size, type, area and season in the California Current System, 1949-1965, coast to 300 n. mi. offshore

Eddy diam (km)		20-100		101-150		151-200		>200		All sizes		%c= $100\,\frac{c}{a+c}$
Eddy type*		a	c	a	c	a	c	a	c	Σa	Σc	
Sector/Season**												
35-38°N	Winter	0.4	0.4	0.4	1.7	0	1.9	2.4	3.7	3.2	7.7	
	Spring	2.8	0.9	1.3	1.3	0.9	0.3	0	1.8	5.0	4.3	
	Summer	3.6	2.3	0.9	1.9	0.9	0.9	0	2.0	5.4	7.0	
	Fall	0.6	1.0	2.7	3.3	0	2.9	0.6	2.7	3.9	10.0	
	Annual	7.4	4.6	5.3	8.2	1.8	6.0	3.0	10.2	17.5	29.0	
	%c	38.3		60.7		76.9		77.3				62.3
31-35°N	Winter	5.0	2.0	1.0	1.1	1.0	3.7	0	7.2	7.0	13.9	
	Spring	3.7	2.3	0.2	1.3	0.9	2.6	0	6.4	4.9	12.7	
	Summer	6.2	1.9	0.3	1.6	0	1.0	0.3	9.2	6.7	13.6	
	Fall	3.0	2.1	1.6	2.4	0	0	0	7.3	4.6	11.9	
	Annual	17.9	8.3	3.1	6.4	1.9	7.3	0.3	30.1	23.2	52.1	
	%c	31.7		67.4		79.3		99.0				69.2
28-31°N	Winter	2.1	0.7	0.4	0.4	1.1	0	1.5	1.2	5.1	2.3	
	Spring	4.1	1.5	2.8	2.4	1.0	1.1	0.4	1.6	8.3	6.6	
	Summer	3.1	0.6	1.4	1.7	2.0	2.2	1.4	0.6	7.9	5.1	
	Fall	1.6	0.5	1.6	1.3	0.3	1.0	0	1.1	3.5	3.9	
	Annual	10.9	3.3	6.2	5.8	4.4	4.3	3.3	4.5	24.8	17.9	
	%c	23.2		48.3		49.4		57.7				41.9
25-28°N	Winter	1.1	1.4	0.7	1.0	0	0.7	0.3	0.3	2.1	3.4	
	Spring	3.2	0	1.8	0.5	0.7	0.9	0.3	0.3	6.0	1.7	
	Summer	4.0	2.2	1.8	2.1	0.3	2.7	0.3	1.0	6.4	8.0	
	Fall	3.3	6.1	2.3	3.3	0	2.0	0	3.8	5.6	15.2	
	Annual	11.6	9.7	6.6	6.9	1.0	6.3	0.9	5.4	20.1	28.3	
	%c	45.5		51.1		86.3		85.7				58.5
All areas 25-38°N		47.8	25.9	21.2	27.3	9.1	23.9	7.5	50.2	85.6	127.3	
	%c	35.1		56.3		72.4		87.0				59.8

*a = anticyclonic
c = cyclonic

**Winter = January, February, March
Spring = April, May, June
Summer = July, August, September
Fall = October, November, December

Eddy characteristics

The Southern California (SC) Eddy is the most resolvable of the eddies in the California Current System by virtue of its large scale and degree of permanence, which usually exceeds the threshold for detection of both the sampling grid mesh and frequency of CalCOFI survey observations. Examples of free eddies at least as large and intense as the SC Eddy have been detected in the main flow of the California Current (e.g. Wyllie, 1966), but have not been measured in detail because of their transitory character.

The SC Eddy is a composite flow pattern. The offshore limb of the Eddy is formed by flow diverging off the coast near Pt. Conception at about 35° N (Hickey, 1979) and extending southward beyond the Cortez-Tanner bank system and is sometimes demonstrated by jet-like flow imbedded in the California Current (Wyllie, 1966). The lower limb occurs as onshore flow between 30°-32° N, likely a result of wind-driven transport (Nelson, 1977).

The nearshore limb is defined by the northward flow along the Bight coast of the SC Countercurrent (Tsuchiya, 1980) which can diverge offshore at Pt. Conception, continue northward along the coast, or episodically disappear. The SC Eddy is quite variable in its extent and circulation strength and may occasionally disappear entirely, for example, at the peak anchovy spawning period in March-April, perhaps even flushing the SC Bight unless replaced by smaller, transitory eddies (Owen, 1980).

It is of interest to compare SC Eddy characteristics with those of large cyclonic eddies elsewhere in the Pacific, particularly one which has been investigated more intensively. The best example of baroclinic doming and eddy upwelling effects is provided by studies of the Costa Rica Dome, produced by a major deflection to the north and east of the North Equatorial Countercurrent as it impinges from the west on the American Continent (Wyrtki, 1964). The Dome is located in the bight of this deflection in a region where nutrients and thermocline both are close to the photic depth (Brandhorst, 1958; Thomas, 1970; Owen and Zeitzschel, 1970a). Its physical characteristics denote a trapped, cyclonic eddy large enough to demonstrate nutrient enrichment effects (Brandhorst, 1958; Broenkow, 1965; Thomas, 1970, 1977) and to detect elevated stocks of phytoplankton, zooplankton and small nekton (Blackburn *et al.*, 1970, Owen and Zeitzschel, 1970b).

Dimensions of several well-studied Pacific eddies and order of magnitude estimates of their mean vertical velocity and volume transport are compared in Table 2 (from Owen, 1980). Despite the varying eddy sizes, intensities and vertical velocities, vertical transport by upwelling is of the same order of magnitude in the SC Eddy, Hawaii Eddy, Costa Rica Dome and in a segment of the coastal upwelling domain 200 km in length (about the same distance along the California coast usually occupied by the SC Eddy). As may be seen from ambient nutricline and photic depths, nutrients are readily available for transfer up through the photic zone in all eddies considered except off Hawaii. Thus, the degree of enrichment and subsequent productivity of the SC Eddy is comparable to that of other major eddy systems. The SC Eddy appears only slightly less effective in total transport of nutrients into the photic zone than upwelling along a comparable segment of the California coastline. As noted above, the SC Eddy receives coastal upwelling products from the nearshore Bight as well as from Pt. Conception and north, although any biological consequences are only poorly understood from rather few and incomplete studies.

SC Eddy effects

During the time of the spring phytoplankton bloom and peak spawning of the northern anchovy (*Engraulis mordax*), the SC Eddy may periodically disappear for a month or more, flushing away the surface waters of the SC Bight. Flushing is episodic in character, most frequent in April (3 of 13 cases). The baroclinic representation of the eddy may also "dissolve" to such extent as to become an indeterminate field of flow. Such dissolution apparently often occurs in the same season as flushing (again, 3 of 13 April cases). The eddy can persist in the absence of the surface countercurrent. The countercurrent typically disappears in April-May, a period when the intensified California Current overrides the coastal countercurrent, to paraphrase Wyllie (1966). This pattern of events is corroborated by independent conclusions from drift bottle release-and-return statistics (Schwartzlose, 1962; Squire, 1977).

Table 2. Parameters of Pacific eddies and California coastal upwelling

	Southern California Eddy[1]	Johnson Atoll[2]	Hawaii Eddy[3]	Costa Rica Dome[4]	Small CCS Eddy[5]	California Coastal Upwelling[6]
Effective obstacle diameter (km)	200	26	100 (wind) 300 (current)	-	-	200 (length**)
Eddy type	trapped	free vortex street	ephemeral wind-forced	trapped	free	(edge eddies occur)
Ambient* or incident flow (cm/sec)	20	60	30	55	20	20
Eddy flow (cm/sec) at 1/2 radius	30	80	50	40	20	-
Radius (km)	100	30	65	200	40	-
Decay time (dy to 1/e)	100	16	>65	-	>14	14
Vertical velocity (m/dy)	0.3	-	0.8(initial)	0.1	-	1.0
Upwelling volume (m^3/dy)	10^{10}	-	10^{10}	-		10^{10}**
Pycnocline elevation $\left(\frac{\text{ambient-dome}}{\text{ambient}}\right)$	0.3-0.5	-	0.4	0.7	0.1	0.4-0.6
Ambient* photic depth (m)	60	100	100	70	70	60
Ambient* nutricline depth (m)	30-70	75	300	40	40	20-60

Sources: [1] McEwen, 1948; Wyllie, 1966; Wyllie and Lynn, 1971; Owen, 1974

[2] Barkley, 1972; Frederick, 1970

[3] Patzert, 1970; McGary, 1955; Frederick, 1970

[4] Wyrtki, 1964; Broenkow, 1965; Bennett, 1963; Owen and Zeitzschel, 1970a

[5] Reid *et al.*, 1963; Owen & Sanchez, 1974

[6] Bakun, 1973; Walsh *et al.*, 1974; McEwen, 1948; Wyllie and Lynn, 1971; Sverdrup and Fleming, 1941; Owen and Sanchez, 1974

* "ambient" refers to condition in absence of phenomenon.
** 200 km coastal strip 50 km wide for comparison with SC Eddy

Spatial variation of community structure and of population densities are evidently affected by the SC Eddy. Changes in community composition take place along flow streamlines: where such streamlines are closed, as in the SC Eddy, successive communities are inevitably juxtaposed. This is apparent from the observations of Allen (1945) and Sargeant and Walker (1948) showing that systematic changes occur in time and space from diatom species ensembles (characteristic of high nutrient injection by recent coastal upwelling) to dinoflagellate ensembles (characteristic of lower nutrient injection into older surface-layer waters). These ensembles were subsequently spatially juxtaposed into what may prove to be a characteristic state due to the Eddy. This effectively demonstrates (perhaps more crudely than actually occurs) the creation of community patchiness by stirring, as defined by Eckart (1948).

Patterns of high phytoplankton concentration which corresponds with that of the SC Eddy are shown by Owen (1974) and by Owen and Sanchez (1974) in terms of surface and depth-integrated chlorophyll a concentrations. These concentration patterns correspond spatially with patterns of higher surface layer and migrating nutrient concentrations of Thomas and Seibert (1974) and with higher zooplankton concentrations in Spring 1969 (Smith, 1974) when the Eddy was fully developed. Together with the evidence for persistence of the SC Eddy, these studies indicate that the observations of Allen and of Sargent and Walker are characteristic (rather than episodic) over the SC Bight. Primary production measurements within the Eddy are too sparse to demonstrate an enrichment effect. A single transect of such measurements (Owen, 1974, p. 98) showed primary production to be about six times greater within the Eddy than outside it. Obviously more observations are needed.

Effects of nutrient washdown into the SC Eddy are not likely confined to only the phytoplankton but certainly involve zooplankton and nekton as well. Arthur (1977) found maximum concentrations of copepod nauplii off the SC Bight at distances corresponding to the offshore limb of the SC Eddy. The maximum zone was associated with colder water, probably entrained from upwelling zones north of Pt. Conception. The pattern suggests that nutrient washdown enhanced reproduction by copepods, a response to their increased food supply.

From plankton surveys over the 1941 spawning season of one population of the California sardine (*Sardinops caerulea*), Sette and Ahlstrom (1948) determined that their eggs and larvae appeared to have been concentrated in an area corresponding closely to that of the SC Eddy and its characteristic elevated diatom densities (Allen, 1945; Sargent and Walker, 1948). This striking local correspondence suggests the susceptibility and possible sensitivity of the sardine stock to the Eddy. The surveys did not cover the entire range of spawning and it is probable that conditions beyond the SC Bight may also have supported spawning areas.

Since the change from dominance of the California sardine stocks to northern anchovy (*Engraulis mordax*), the CalCOFI plankton surveys have covered the spawning time and area of the anchovy. These have revealed (Smith, 1978) that the region inclusive of the SC Eddy, comprising about 12% of the spawning area of the anchovy's central subpopulation, contained 48% of their larvae on the average (1951-1975) and since 1966, 64%.

Berner (1959), in his study of food of anchovy larvae, noted that areas where larvae were found to be actively feeding corresponded to those of the copepod nauplii maximum as described by Arthur (1956). Comparison of areas of active larval feeding in the SC Bight, with corresponding charts of baroclinic flow (Wyllie, 1966, pp. 76, 79 and 82) show that the area of feeding larvae corresponded with the inshore limb of the SC Eddy, although Arthur (1977) subsequently showed that maximum concentration zones of copepod nauplii coincided with the SC Eddy axis or its offshore limb.

Brinton (1976) studied the population biology of *Euphausia pacifica*, a dominant species among the larger zooplankton of the SC Bight. He identified the SC Eddy and its associated upwelling regimes as a reproductive refuge for an identifiable population of the species.

Population persistence in benthic-dwelling organisms with planktonic life-history stages (usually larval) depends on their deposition at the end of the planktonic stage in waters shoal enough to permit survival on the sea bottom. Off the Californias, where flow frequently diverges from the coast, such populations depend on eddies and meanders in the mean flow to return a sufficient number of their meroplankton to appropriate habitat. Examples of this dependency include populations of the spiny lobster, *Panulirus interruptus* (Johnson, 1960) and the red crab, *Pleuroncodes planipes* (Longhurst, 1968). Both organisms spend extend periods as plankton in their early life history, yet maintain stationary and localized centers of the adult populations.

PATTERNING BY FRONTS

Within and between eddy systems, discontinuities known as "ocean fronts" occur which provide identifiable sites for smaller scale and more specific biological activity of likely significance to larval and adult fishes. Ocean fronts are line zones of laterally convergent flow that intensify vertical water motion. They occur singly or in series. Patterning of biological substances can occur mechanically, e.g., concentrating or dispersing organisms that move vertically through advection or convection. Patterning also occurs by indirect mechanisms: local nutrient enrichment and behavioural properties account at least qualitatively for localized responses to fronts by organisms including some types of phytoplankton, zooplankton, fishes, sea snakes, bird and whales.

Scales of variation of plankton tend to be much smaller in the presence of fronts as compared to patterns impressed by eddies. A basic and attractive tenet is that vertical displacements have greater ecological effects than similar horizontal displacements because environmental gradients of light, pressure, temperature, salinity, oxygen and nutrients are by far the steepest in the vertical dimension. Vertical motion in fronts is often vigorous and highly localized, whereas that in eddies is slower and spread over much larger areas. For this reason, coherent horizontal gradients of temperature, salinity and food supply are correspondingly sharper across convergent flows than across eddies. Their respective biological effects occur on accordingly disparate scales.

Scales on which ocean fronts have been observed to occur and to pattern organisms range laterally from 1 m - 10^5 m, persisting (depending on size) from hours to virtual permanence. The smallest-scale fronts are by no means ecologically insignificant since they may extend (in diverse patterns) over large ocean areas.

B̄enard and Langmuir Fronts

The smallest coherent frontal patterns that have been noted to collect organisms in the open sea were attributable to the B̄enard mechanism. B̄enard circulation occurs when cooling and salt gain through evaporation make surface water rapidly more dense: thermohaline circulation cells form a honeycomb pattern of surface convergences as the denser water exchanges with the less saline and warmer subsurface water. The resulting honeycomb pattern is easily deformed by wind or subsurface shear to form a series of small elongate, parallel fronts.

Surface convergences of this sort reported by Owen (1966) penetrated to less than a metre in depth, extended visibly for more than 30 m in unbroken length and were spaced at intervals of about 1.5 m. The patterns persisted in the absence of wind for at least two days. Taken singularly, such "micro-fronts" would have little ecological impact. However, this particular frontal system observed by Owen (1966) extended over several hundred km^2. Such fine-scale patterns can produce widespread alteration of concentration patterns and, presumably, concentration-dependent biological processes. In this instance, the surface convergences were marked by red bands less than 10 cm wide that consisted of upward swimming oikopleurans that had been highly concentrated in the upper 5 cm of the convergence planes. Their still-water swimming speed of about 0.2 cm/sec was used to set an upper limit on downwelling water speed in the convergence planes.

Under freshening and sustained winds, convergence systems of the better known and (usually) larger scale Langmuir circulation either develop into patterns like B̄enard cells or create their own patterns, detectable as parallel windrows. These windrows lie along the wind axis and are often marked by assemblages of floating organisms or substances. These are swept by convergent surface flow to the frontal zones. Trapping efficiency of buoyant materials is virtually 100% under steady winds of constant direction. Surface convergences can become strong enough on occasion to submerge even highly buoyant

Sargassum weed, requiring a downwelling circulation of 5-7 cm/sec (Woodcock, 1950). Organic films on the sea surface are also rapidly collected along such convergences to give windrows their most common streaked appearance. Under lower winds, collected oils dampen capillary waves to give the windrows the appearance of parallel slicks. At higher wind speeds the organics can be partly frothed and convergences appear as foam lines.

The size and circulation strength of these convection cells increase with time and wind speed. Spacings between convergence lines from several metres to over 100 m are typical, and downwelling speeds may exceed 10 cm/sec. Depth of penetration is some fraction of the distance between convergences, usually half or somewhat less.

Extant theories that attempt to account for the Langmuir circulation include stability of vertical shear in the water, forcing by atmospheric vortices, wind-oriented thermal (Bēnard) convection, wind profile modification by surface films, lateral radiation pressure on surface films, convergence of wave trains (reviewed by Scott et al., 1969), and vertical decay of surface wave oscillations (Faller, 1969). Failure of data to support or rule out any single mechanism led Scott et al. (op. cit.) to conclude that combinations of mechanisms could occur. A subsequent study (Harris and Lott, 1973) lends support to the possibility of development of Bēnard cells into Langmuir cells: mean downwelling velocities ranging from 2.1 to 9.4 cm/sec in Langmuir convergences correlated well with wind speed during net surface cooling but not as well during net surface heating. Despite the lack of agreement on mechanisms, the Bēnard-Langmuir circulation is now widely held to be an important mechanism for vertical transfer of heat and substances in surface waters of lakes and seas. Large temporal variations, with a strong diel component (Woods, in press) may be expected in both Langmuir and Bēnard circulations.

The theoretical and mathematical description of particle trajectories in cellular convections was formulated by Stommel (1949) and subsequently elaborated to include swimming (e.g., Stavn, 1971). Direct observations to date confirm the applicability of the model to real particles and plankters in such circulations, despite the rather large difficulties of field measurement and the less-than-ideal behaviour of both the fluid and plankton.

A number of field studies confirm the effectiveness of the Langmuir circulation in collecting and patterning organisms and substances. The most visible examples involve buoyant animals and substances such as Physalia (Woodcock, 1944), Sargassum weed (Faller and Woodcock, 1964; Woodcock, 1950) and surface films (Szekielda et al., 1972). Sutcliffe et al. (1963) demonstrated that whitecapping and perhaps other wind action converts dissolved organics to particulate form available to zooplankton, and that a downwelling Langmuir convection, at 3-6 cm/sec, produced subsurface concentration zones of these particulates. The soluble inorganic phosphate concentration was also shown to be higher in such particulates. Sutcliffe et al. (1971) show, by detecting an increase in particle concentrations with increase in wind speed, that the process is highly effective. They found peak production to be particles of 6 um diameter. Higher concentrations of particles 2-13 μm diameter were shown to occur below convergence zones.

Patterning of phytoplankton and microzooplankton by Langmuir circulations has been more widely reported than one would expect from the mismatch of their reported speeds. Bainbridge (1957) reviews several observations of dinoflagellate concentrations in Langmuir scale patterns. The mobile and prolific ciliate Mesodinium rubrum, which can "zig-zag" at speeds up to 2 mm/sec and also occur in bloom ("red-water") concentrations, has been reported to gather in Langmuir convergences. Powers (1932) found Mesodinium in windrows off Maine, and Bary (1953) observed windrows of these ciliates to orient along a changing wind axis in New Zealand. Packard et al. (1978) describe Mesodinium windrows spaced at 100 m intervals under 10-20 knot winds, and their dispersion through the water column at winds over 30 knots.

Patterning of larger zooplankton in Langmuir circulations is less apparent and notoriously difficult to sample. The best examples of Langmuir patterning of zooplankton thus are from lakes, where populations of cladocerans and copepods migrate vertically into vortices in the epilimnion and concentrate in convergence planes (e.g., George and Edwards, 1973). Survival of Peru's larval anchoveta has been proposed by Ware et al. (in press) to be enhanced in the presence of small-scale patterning of their food supply in windrow circulations.

Internal wave effects

Internal waves, responsible for surface banding on continental shelves, do not actively produce organism patterns but may modify extant patterns. Interaction of waves with bottom topography, current shear, and diminished vertical stability can produce instabilities (and breaking waves) that disrupt pattern. Internal waves may interact with current boundaries and shelf-break fronts. Curtin and Mooers (1975) presented measurements that indicated generation of large amplitude, high frequency internal waves by breakdown of the semi-diurnal internal tide at the shelf-break front off Oregon. These induced major perturbation of a sonic scattering layer (organisms) inshore of the front. Earlier, Yasui (1961) presented a theoretical framework arguing for propagation of tidal-period internal waves along fronts of the sort encountered as Shiome, fronts due to current confluence, which are zones of high lateral shear as well as vertical circulation. Localized interaction between internal waves and eddies in mid-ocean also has been detected (Frankignoul, 1976), which may affect rates of vertical diffusion. As yet, these phenomena seem to be unexplored but may be expected to modify effects of fronts on populations of organism. Kamykowski (1975), for example, presented a mechanism by which phytoplankton can interact with the semi-diurnal internal tide to produce patterns of species concentrations. The biological result of internal wave interaction with fronts or eddies is obscure but may be significant. Internal waves are sensitive to current shear and to vertical density gradients, both of which vary at fronts and in eddies. It will not be surprising to find evidence of biological responses to these dynamic physical processes if adequate sampling techniques can be devised.

Tidal fronts

Simpson and Pingree (1978), Pingree et al. (1977) and Pingree et al. (1974) describe cases of genesis and decay of shallow sea fronts by variable tidal mixing on the European continental shelf. Surface convergent fronts of considerable physical and biological activity occur in zones where water types of different mixing histories impinge. Vertical mixing was induced in shallower waters by frictional dissipation on the bottom interface of (mainly) the principal lunar tidal component of flow and stratified cooler waters. In some areas of the shelf, such vertical mixing is sufficiently vigorous to prevent or override density stratification. Where tidally-mixed shoal water contacts stratified deeper water, a convergent front occurs. Thermal images of the Celtic Sea from the NOAA-5 satellite indicated the broad extent of tidal fronts like those examined in these studies have shown the genesis of a cold eddy from a frontal meander. Shipboard measurements of a similar front (Pingree et al., 1977) show its response to neap and spring tide cycles and its effect on phytoplankton chlorophyll concentrations in the stratified water well beyond the front. The study suggests that blooms of a dinoflagellate population offshore were caused by periodic release of nutrients from the destratified inshore side of the front by decay of the front during neap tides.

Admixture of water types at shelf fronts locally stimulates phytoplankton photosynthesis and thus sustains higher phytoplankton concentrations in the frontal zones. Savidge (1976) and Savidge and Foster (1978) describe such a process from surface measurements of chlorophyll, temperature and photosynthesis along transects on the European shelf between Ireland and Wales.

Zooplankton concentrated in shelf fronts is also commonly observed but descriptions from physical and biological measurements in such fronts are rare. Pingree et al. (1974)

describe activity in a vigorous tidal front of 15 km extent in the English Channel from temperature, salinity and current measurements and from direct underwater and surface observations of its effects on organisms and substances. Surface net hauls in the front showed greater concentrations of copepods, crustacean meroplankton, the euphausiid Nyctiphanes sp. and young fishes.

Plankton concentration at the front was confirmed by sub-surface visual observation. Underwater observation of motions of plankton and of dye injected at several depths also confirmed the turbulent, convergent character, which was apparent from temperature and salinity structure and from drogue measurements. The list provided of animals associated with floating macrophytes concentrated at the front consisted of a variety of post-larval fishes and crustacean species. Puffins, shear-waters and terns were seen feeding along the front, which also collected debris and oil lumps. The authors remark on the similarity of this front and its biota to the large, deep-ocean fronts described by Beebe (1926) and Amos et al. (1972).

Shelf-break fronts

Fronts of large extent commonly occur in the general vicinity of the shelf-break, i.e., where the slope of continental shelf steepens to become the continental slope (generally at about 100-300 m depth). Mooers et al. (1978) usefully distinguish between prograde fronts, those that separate more saline shelf water from offshore water; and retrograde fronts, those that separate less saline shelf water from offshore water. Shelf waters of both types are colder than offshore waters.

Prograde fronts arise by upwelling on the continental shelf. Seasonal and episodic wind-driven upwelling is characteristic of eastern boundary current systems, but occurs inshore of western boundary currents as well, where upwelling occurs by topographic deflection of currents. Retrograde fronts are due to shelf-water dilution from terrestrial runoff and thus predominate off large terrestrial water sheds. Their incidence and intensity usually vary with season.

Upwelling fronts

Prograde shelf-break fronts off upwelling zones bound the plankton-rich shelf waters. There is a dearth of studies that demonstrate higher plankton concentrations in these fronts than inshore, at least in part because field studies have been concerned more with the upwelling system as a whole and do not sufficiently sample frontal interfaces. Packard et al. (1978) describe the incidence and habitat of the pigmented ciliate, *Mesodinium rubrum* in an upwelling zone off Baja California. Surface-layer concentrations of this ciliate at prograde fronts appear to be facilitated by characteristics of its environment in combination with its phototaxic behaviour, rapid reproduction rate and ability to use both inorganics and organics for food.

Laurs (unpublished thesis), working with measurements of concentration of phytoplankton zooplankton and micronekton in and beyond the Oregon upwelling system, detected higher stocks near the frontal zone and in an anticyclonic eddy (phytoplankton only) outside the front. Bang (1973) describes a strong upwelling front extending northwest off Cape Town in the eastern boundary current off South Africa. Mixing cells occurred and episodic overturn at the front produced subthermocline sheets of homogeneous water. Higher concentrations of large zooplankton or micronekton were detected at the front by fathometer records.

Albacore make annual trans-Pacific migrations to feed on relatively high concentrations of large plankton and small fishes in the California Current, seaward of the coastal upwelling zones. The offshore extent of these upwelling zones are frequently denoted by prograde (upwelling) fronts. Albacore caught, tagged with ultrasonic transmitters and subsequently released, were tracked in the vicinity of such a front off Monterey Bay, California (Laurs *et al.*, 1977). Tracking results showed that such temperature fronts can influence local concentration of albacore; sonically tagged albacore moved about in the vicinity of the front, then moved away when the front weakened as upwelling ceased. These albacore also were seen to move more slowly when crossing fronts and to spend little time on the colder side ($T < 15^{\circ}C$), indicating a thermal barrier effect which would result in their collection at fronts. The enriching effects of large cyclonic eddies that predominate outside upwelling zones, and of eddies that transport substances away from upwelling zones (Owen, in press B) may also support higher forage levels beyond shelf-break.

As demonstrated for tidal fronts, an important aspect of upwelling fronts may be their periodic relaxation, their decay, and subsequent release into offshore water of nutrients and plankton previously accumulated in the shelf water. Frontal relaxation occurs upon cessation of upwelling. This can occur either seasonally or episodically depending on the wind system. Breaching, or destructuring dissipation occurs more locally than does relaxation. The causes of breaching have not been defined but likely involve meanders and eddies formed by local instabilities of frontal currents, impingement of eddies from outside the fronts, and perhaps wave interactions with the fronts. When clear weather permits, breaching is clearly evident in thermal images of sea surface temperature fields off California transmitted from satellites. Bernstein *et al.* (1977) demonstrate the possibility of using such infrared images to follow the genesis, lysis and incidence of fronts as well as eddies and upwelling zones in the California Current System.

Estuarine fronts

Retrograde estuarine fronts exhibit salinity gradients, because freshwater sources dilute surface waters on one side of such fronts. Iizuka and Arie (1969) showed concentrations of *Trichodesmium* (flagellate) for 80 km along an estuarine front off Japan. LeFevre and Grall (1970) showed similar convergent aggregations of *Noctiluca scintillans* off Brittany and also emphasized local competition that was apparent between *Noctiluca* and copepods for diatoms in the convergence area.

Owen (1968) studied effects of the Columbia River plume, which albacore encounter in their summer arrival off Oregon. Based on research vessel catch rates and oceanographic data, results showed that albacore moved through the outer plume boundary, defined by the $32.2^{0}/\infty$ isohaline that defined the outer boundary of the salinity gradient of the plume-sea front (Owen, 1967). Albacore catches were somewhat lower in mid-plume than in the vicinity of its frontal limits, indicating an attraction to forage in fronts per se and possibly a combined attraction/aversion to the warmer temperatures/lower salinities of the plume core. Catch rates were higher near the seaward limit than inshore, where even stronger thermohaline fronts resulted between plume coastal upwelling zones.

Tsujita (1957) showed seasonal cross-shelf movements of stocks of the Japanese sardine off western Japan. Spawning and hatching occurs at depth in oceanic water off a retrograde (estuarine) coastal front. Larvae move shoreward through the shelf-break front, seek nearshore feeding grounds, grow to 7-10 cm length and diffuse seaward in summer in the upper layer of the shelf waters.

MICROSCALE PLANKTON PATCHINESS

Patterning of plankton occurs on the sub-metre scale. Cassie (1959a, b) demonstrated high variation of plankton concentrations at the sea surface, and Owen (in press b) showed similar variations at sub-surface depths. The role of circulation in the patterning process is obscure, particularly since this approaches the scale of turbulent dissipation. This section discusses some new measurements made to determine if small predators and grazers encounter food patches in excursions of less than 2 m extent. Variation in food supply available to fish populations is commonly examined to help determine causes of large interannual fluctuations frequently experienced in the availability of fish to fisheries. Yet concentrations of food of first-feeding northern anchovy (*Engraulis mordax* Girard) seem frequently to be too low in the California Current System for larval survival and growth (Lasker *et al.*, 1970). This may be because conventional sampling with plankton nets, which integrate over depth, distance and volume, has little relation to the comparatively tiny volumes searched by single larvae (Hunter, 1972). Survival of such larvae may, in fact, depend on the existence of food particle patchiness on scales considerably less than 10 m and 1 week (Vlymen, 1977).

Regions sampled

Southern California Bight waters tend to high vertical stability by virtue of characteristically slow flow (reduced shear) and year-round net heat gain, except in December, by the ocean's upper layer (Clark *et al.*, 1974). The mixed layer is relatively shallow (<30 m), due to the combined influences of wind shattering, heat gain, the California Current and the Southern California Eddy. Large temperature gradients predominate over salinity gradients in determining vertical stability. Maximum stability occurs in the upper pycnocline in the absence of steady winds. These characteristics are favourable to the development of small-scale patchiness but are episodically reversed by storm winds of a few days duration, which destroy shoaler layering (Lasker, 1978). Episodic upwelling, internal waves, and eddies may destratify the water column locally along the narrow shelf of the Southern California Bight margain and in even more restricted areas near islands and capes.

The region studied off Peru is functionally similar to the S.C. Bight in having a shoal pycnocline, destratification on the shelf, and high production rates of forage and fish. Differences between the sampled regions are mainly of magnitude: Peru's shelf is 1-2 orders of magnitude broader, the margin is more exposed to storm activity, and processes of destratification are more dynamic, somewhat more consistent, and more broadly effective than in the SC Bight. The role of eddy processes in the Peru region is unassessed. Well-defined prograde fronts are found on and near the Peru shelf. These frequently separate stratified from unstratified zones but cellular fronts also occur on smaller scales, e.g. Bénard-Langmuir on sized cells.

One would thus expect off Peru both a lesser degree of vertical microstructure of plankton and environment, and a lesser need of such microstructure by the larval fishes due to the increased general productivity compared to the Southern California region.

Microscale measurements

Samples to assess microscale patchiness at each site were obtained using an array of water samples on a varied frame. The micropatch sampler (MPS) sampled either in the mixed layer or in the upper pycnocline in the main chlorophyll maximum layer, as defined by pigment fluorescence in a water stream provided by continuously lowered pump and hose. Clamped either vertically or horizontally to the ship's hydro-wire and lowered to the depth desired, the MPS captured water at ten intervals on 20 cm centres in 5 cm (i.d.) tubes of 600 ml capacity by simultaneous messenger-activated release of lanyards which restrain ball valves from their seats at either end of each sample tube. Replicates were obtained on some casts by strapping another sample tube alongside the original. When sampling vertically, vanes oriented the sample tube mouths to face a current of ~50 cm/sec induced by moving the ship slowly ahead. This minimized vertical mixing of the water by the MPS. When sampling horizontally (tubes vertical), the tubes were closed while raising the array. Water was aliquoted for various analyses from the well-stirred contents of the MPS tubes upon recovery aboard ship. Plant pigment determinations were made by the fluorometric method on acetone extracts, particle concentrations by Coulter T_A, nutrients by autoanalyzer and salinity by inductive bridge. Samples for microscope analysis were preserved in <5% buffered formalin spiked with strontium chloride. These were counted ashore by the sedimentation method of Utermohl (1931).

Microstructure of organism populations

Results of microscope counts are summarized in Table 3 as coefficients of variation, V = 100 x variance/mean, of concentrations determined over the 10 intervals sampled to represent the 2 m span. Where replicate samples were counted, average values between replicates were used in the computation. Coefficients are shown for population counts exceeding 10 in at least one of the samples in the set. Trends (i.e. mean gradients) over the 2 m span are represented by the coefficients, as are variations within the span (i.e. deviations from mean gradients). Both sources are taken to indicate microstructure degree because sampling was done in the absence of conventionally detectable biological gradients (i.e. in mixed layer and chlorophyll maximum). The V statistic was chosen because it scales variances for comparability and because it is widely used and understood. A measure of sampling and counting error is provided from counts on four MPS sets each consisting of five replicate sample pairs. The average coefficient of variation between replicates for 15 taxonomic groups counted was 10.9 (range was 4.0 - 18.5), not including the coefficient for ciliates associated with marine snow at two sites (7703J-MS1, MS2).

V-coefficients are considered to indicate significant microstructure if they exceed the average replicate V-coefficient by at least a factor of 3, Table 3 shows that:

- Microscale patchiness is apparent ($V > 33$) at all but one of the 13 Southern California Bight sampling sites and at both Peru sites for one or (usually) more kinds of organisms enumerated.

- Most types of organisms suitable as larval anchovy food display significant degrees of microaggregation. Non-food organism types are also aggregated, in many cases to an even greater degree, and not necessarily in the same zones as the presumed food organisms.

- Vertical profiles in the upper mixed layer of the SC Bight (the latter defined by absence of density gradients determined from standard STD casts) showed significant microscale patchiness for 5 of 8 food types and 3 of 8 non-food types at one site or the other, both occurred during the anchovy spawning season under calm wind conditions. At the shelf edge off Peru, in the lower part of the mixed layer under 20 kt winds, microscale patches of ciliates, copepod eggs and the diatom *Corethron* were detected.

- Microscale variation was usually greatest in the pycnocline and in the vertical axis for most food and non-food types alike (but see *Exuviaella* sp. C - this flagellate species behaves rather differently on the microscale, being more randomly dispersed vertically than horizontally in the pycnocline and apparently capable of forming small patches in the mixed layer).

- Non-motile or weakly motile organisms (cf. *Nitzschia*, *Thalassiosira* and pennate diatom categories) may show as much or more patchiness as motile organisms (cf. *Exuviaella*, *Prorocentrum* and ciliate categories).

- There is no evidence for a difference in degree of vertical microstructure in the pycnocline between periods of peak and minimal spawning activity (mean V = 49.3 and 50.0, respectively). This is perhaps partly due to too few comparable categories since species composition changed between periods sampled, complicating relevant interpretation regarding appropriate larval anchovy food.

Table 3. Coefficients of variation of organism concentrations sampled at ten 20-cm intervals (interval replicates averaged where obtained) in the mixed layer and upper pycnocline of the coastal shelf of the Southern California Bight and Peru (7711).

		Vertical casts in pycnocline at chlorophyll maximum layer									$\bar{V}$	Horizontal casts in pycnocline			$\bar{V}$	Vertical casts in mixed layer			$\bar{V}$
TOP DEPTH (m)		22	23	25	29	20	20	14	20	15		17	18	21		10	10	15	
DATE (Year/Month)		7509	7509	7509	7509	7603	7603	7703	7708	7711		7603	7603	7603		7603	7703	7711	
MPS No.		1	2	4	5	1	5	2	1	3		3	10	11		2	1	2	
FOOD TYPES	Exuviaella sp.C					22.7	17.3					27.4	29.1	21.8		12.8	76.6		
	Oxytoxum septrum						27.7												
	Prorocentrum gracile	69.8	52.6	138.4		45.4										37.6			
	Peridinium (2 spp.)					50.9							19.2			25.4			
	Peridinium minutum					174.1		25.0					35.2			35.5	21.2		
	Cochlodinium catenatum	28.4		51.2	44.9				22.0										
	Gymnodinium sp. S					22.2													
	Torodinium robustum								29.8										
	naked flagellate 30x50 µm					67.4			14.5			27.3	21.4	17.3			41.6		
	tintinnids 100 µm						98.6			51.9						22.2	34.2		
	free ciliates			54.6	44.2	64.1	11.5	63.2				26.2	14.3	24.4		9.9	23.4	43.2	
	copepod nauplii					32.0	25.4						29.6			10.7	31.8		
	Prorocentrum micans									59.5									
	Copepod eggs, 35-80 µm									30.7	49.6				24.5			123.0	36.6
NON-FOOD TYPES	Nitzschia seriata					51.8	44.9						35.7			29.2			
	Eucampia zoodiacus							115.7								31.0			
	Thalassiothrix frauenfeldi															25.1			
	Thalassiosira sp.A							27.3											
	pennate diatom 30 µm			158.2	92.2														
	silicoflagellate			55.3	60.4														
	Ceratium kofoidii	39.1				58.4						39.2							
	Dinoflagellate spp. 5x10 µm					27.9							31.1			27.0			
	Pseudoeunotia doliolus	95.7	10 .6	56.8															
	Thalassiosira sp.B								28.9					37.3					
	Skeletonema costatum															40.1			
	pollen grain 70x40 µm																65.6		
	oikopleurans															52.4			
	Noctiluca sp.					29.0	21.2									21.5			
	Corythron sp.																	33.9	
	Pleurosigma elongatum									59.5									
	Pleurosigma nicobaricum									86.9	63.9				33.5				36.2

In the 15 microsampler sets enumerated by microscope, 20 species of phytoplankton, 6 categories of microzooplankton, and 4 size categories of detritus were sufficiently populous to examine their microscale variation. Microstructure occurred in 94% of profiles of phytoplankton species, 92% of microzooplankton profiles, and 85% of detritus profiles in 3 size categories ranging from 16 to 200 µm.

The maximum concentrations of food and non-food organisms do not usually coincide on the microscale. A characteristic experience is shown in Figure 1, taken from a vertical MPS cast in the pycnocline, in the vicinity of the main chlorophyll maximum. This effect may augment the increase in availability of food organisms due to microstructure by reducing local abundance of undesirable strike targets in zones where food organism concentrations are highest. The argument assumes varying degrees of distinguishability and desirability among the food types by the fish larvae, as there are no consistent patterns apparent between food and non-food organism distributions on this scale.

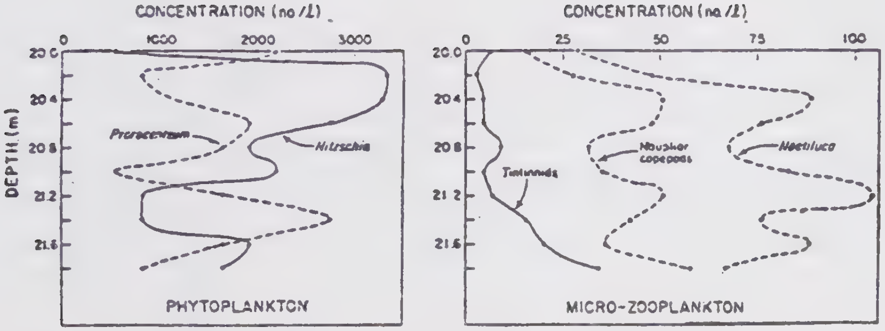

Figure 1. Microscale variation of larval anchovy food and non-food organisms in the pycnocline of the Southern California Bight

Concentrations of suitable food in one MPS cast of 13 analyzed from the SC Bight exceeded the "critical concentration" criteria of Lasker and Zweifel (1978) for survival and growth of anchovy larvae. This incidence would likely be higher if (1) all food type organisms had been enumerated rather than those selected only for clear identification and abundance, or if (2) high plankton standing stock had been among criteria for choosing sampling sites.

Patch shape

Results of four casts made horizontally at depths comparable to those of vertical profiles permit a rough estimate of the *in situ* shapes of particle patches. Variation in concentration of the more numerous components of the microplankton community present averaged three to five times greater in the vertical sets than in the horizontal sets, as measured by the coefficient of variation, $s/\overline{X}$, of counts made on these components. This leads me to speculate that populations were concentrated in partly overlapping lenticular patches with horizontal dimensions three to five times greater than vertical dimensions. This geometry provides an interesting contrast with shapes of plankton patches discerned on larger scales, whose characteristic vertical dimensions are reported in metres and horizontal dimensions are reported in km (e.g. Bainbridge, 1957). This indicates a marked tendency towards isotropy with diminishing scales and bears further investigation for confirmation.

The observations suggest no simple relationship between organism types, but show a large degree of variation on short intervals. Results confirm Vlymen's (1977) postulate that some degree of small-scale patchiness (on the scale order reported here) must necessarily occur to support even the minimum fraction of anchovy larvae surviving to recruitment size. The results also suggest sampling precautions to be taken wherever minimum or maximum plankton concentrations need to be known or where "critical concentrations" need to be detected.

Microstructure of bulk properties and organisms

Vertical sampling of the water "column" by water-capturing devices at intervals usually spaced more than 5 m apart or by continuously-lowered pump and hose, both underestimate the *in situ* variations of concentration and thus lead to underestimates of the maximum concentrations actually present. The degree to which this can occur is shown in Figure 2, where a small inversion in plant pigment concentration, detected *in vivo* by fluorescence of a sample stream from a pump profiling system, was resampled within 5 minutes by the microsampler array and acetone extracts of filtered samples analyzed by fluorometer for chlorophyll and phaeopigment concentrations. Unlike determinations from filtered, extracted samples from the microsampler, the *in vivo* measurement does not differentiate between chlorophyll a and phaeopigment (photosynthetically inactive degradation products of chlorophyll). Hence both are shown in the insert. Noting that the pigment concentration scales are the same for pump and microsampler array, the degree of averaging by the pump system is apparent: the variation of pigment concentration over the 0.6 m depth interval was an order of magnitude greater as sampled by microsampler than by the pump. This case displays the greatest disparity yet encountered between pump and MPS profiles of plant pigment.

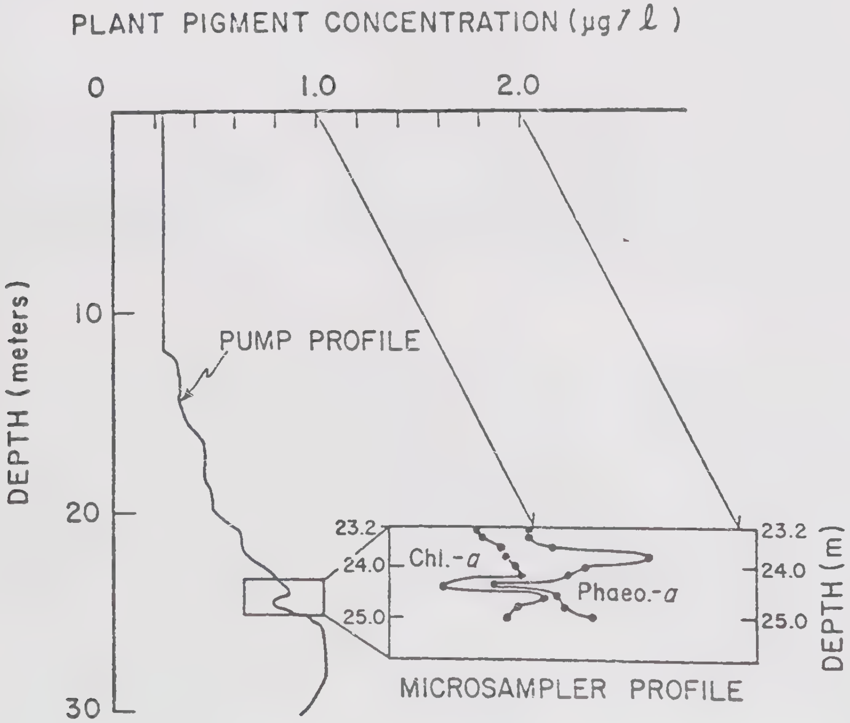

Figure 2. Comparison of small-scale change of phytoplankton pigment concentration by pump profiling and by 20-cm discrete sampling in California coastal waters. Pigment concentration scales are the same for both displays.

To date, 33 vertical and 4 horizontal microprofile sets have been obtained from mixed and stratified coastal waters in the Southern California Bight and on the Peru shelf under all but full-storm conditions. Of these, all except a horizontal set made in the mixed layer exhibited variations beyond sampling and measurement error of one or more of the parameters measured over the 2 m interval. As examples, two microprofile sets are shown in Figure 3. Also shown (lower panel) are concentration profiles of chlorophyll, an integrative measure of phytoplankton density; phaeopigments, photosynthetically inactive derivatives of chlorophyll; particulates 16 to 160 µm diameter, indicative of detrital particle load in this region; and inorganic nitrate, important for phytoplankton growth. Both were obtained from the SC Bight in the density-stratified portion of the water column where the bottom depth was about 200 m. They were selected because most parameters in these two sets displayed small-scale variations that exceeded sampling and measurement error. Greater variation existed within any single parameter in other sets. Concentration profiles of a motile phytoplankter, *Exuviaella* sp. C; oligotrich ciliates; and copepod nauplii were selected to depict microscale variations of species and of functionally similar groups (upper panel). Each is a food item of larval anchovy.

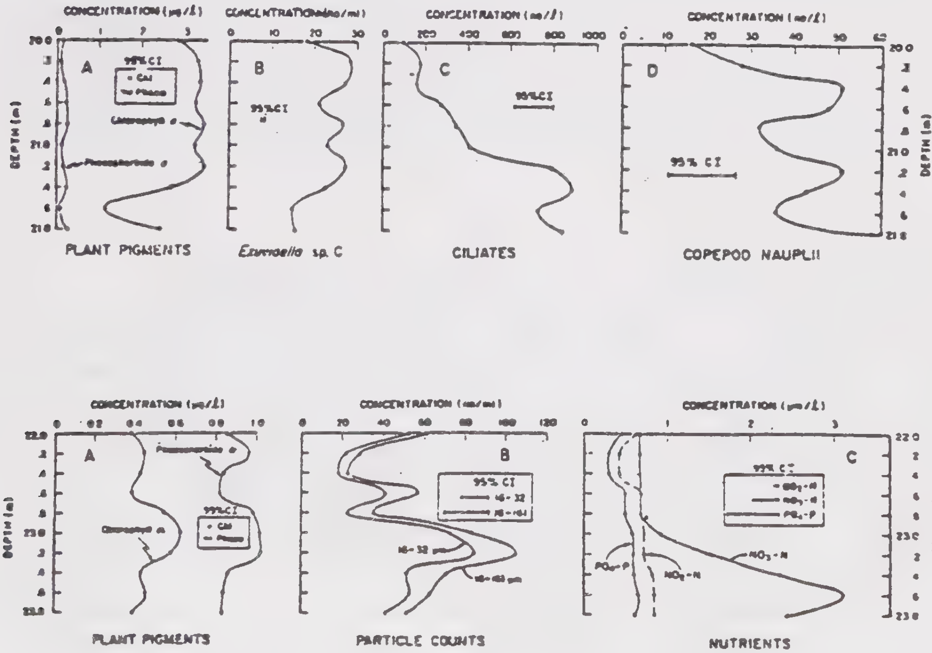

Figure 3. (Upper panel). Microscale variation of plant pigments and three organism types from the pycnocline in the Southern California Bight in March (7603/MPS-1). (Lower panel). Microscale variation of plant pigments, particles and nutrient salts from the pycnocline in the Southern California Bight in September (7509/MPS-1).

Results of a September cast in the SC Bight demonstrates the small-scale variation commonly present in plant pigments, particle concentration and nutrients. The incidence of microstructure was high; significant fine-structure existed in 16% of 22 particle profiles and 11 of 21 nitrate profiles and in both of two ammonium profiles. The particle coincidence of particle and plant pigment maximums centered at 23.2 m is fortuitous; virtually all particle profiles were independent of the corresponding plant pigment profiles (15 sets). Incidence of plant pigment microstructure was quite high. All 23 sets analyzed showed variation of chlorophyll concentration indicating microstructure of the phytoplankton community as a whole. Fewer (19%) showed cm-scale variation of phaeopigments. In the set shown in Figure 3 (lower panel), the phaeopigment profiles resembles that of chlorophyll a. However, of 23 such profiles, 14 exhibited unrelated profiles of chlorophyll and phaeopigments and 4 exhibited inverse relationships. This inconsistency demonstrates a degree of independence on the microscale which is not apparent in pigment concentration profiles from the usual sampling intervals of 5 to 10 m. This independence may be due to local effects of grazing or to differential rates of local production and sinking of the two particle types. These measurements thus may reflect the spatial scales on which these processes are first apparent.

Microstructure was not, of course, always detected. Sample series from the wind-mixed upper layer of the SC Bight showed less variation of organisms, particulates and nutrients than did sample series from density-stratified waters. However, significant microstructure of motile and non-motile organism populations, as well as of detrital particles, was detected in 2 of 4 casts made within the mixed layer in the absence of measurable density gradients, when mixing by wind was not in progress. The nutrient salts phosphate and nitrite-nitrate exhibited low incidence of microscale variation over distances less than 2 m in both regions sampled. Widely varying values of silicate concentration suggest microstructure for that nutrient but occasional wide disagreement between replicate samples vitiate the case for silicate microstructure. Salinity (5 sets) varied monotonically in the presence of nutrient and organism microscale variation. Temperature microvariation was not measured.

Peru microscale

Microstructure of biological materials apparently occurs under a variety of environmental conditions. Off Peru during Project ICANE (Doe, 1978), MPS-3/7711 sampled 5 km from shore near Chimbote below a surface layer stabilized by surface layer heating after recent weakening or cessation of upwelling. Large quantities of the "weed" diatom *Chaetoceros* were present at the surface and at the sampled depths. Microstructure of two types was evident among populations enumerated from 15-17 m depth. Concentrations of the diatoms *Pleurosigma elongatum* and *P. nicobaricum* exhibited nearly monotonic, stepwise decreases with depth (Fig. 4, upper panel), whereas spheres, tintinnid ciliates and *Prorocentrum micans* exhibited yet smaller-scale variations by pronounced maxima and minima between 15 and 17 m (Fig. 4, lower panels). Nutrient salt concentrations, nitrate-nitrite, ammonia, phosphate and silicate at this site exhibited no microstructure (Fig. 5). Particle concentrations, by Coulter Counter, indicated significant microstructure of particulates likely dominated by detrital substances (Fig. 6). By contrast with stabilized conditions at the coastal site, MPS-2/7711 sampled 10 km seaward of the shelf-break at about the same latitude (9°S) as MPS-3. More labile conditions prevailed at this site; MPS-2 sampled from 15-17 m in the virtually isopycnal layer that extended from the sea surface to 21 m depth under 20 kt winds. Standing stocks of phytoplankton were less than at the coastal station, tintinnids were supplanted by oligotrich ciliates, and copepod nauplii were more abundant.

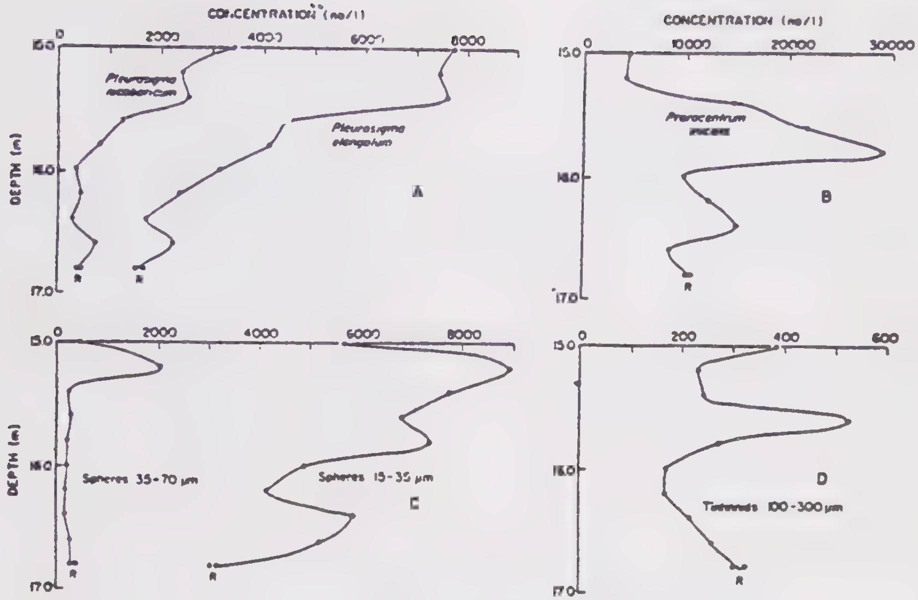

Figure 4. Microscale variation of larval anchovy food and non-food organisms in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

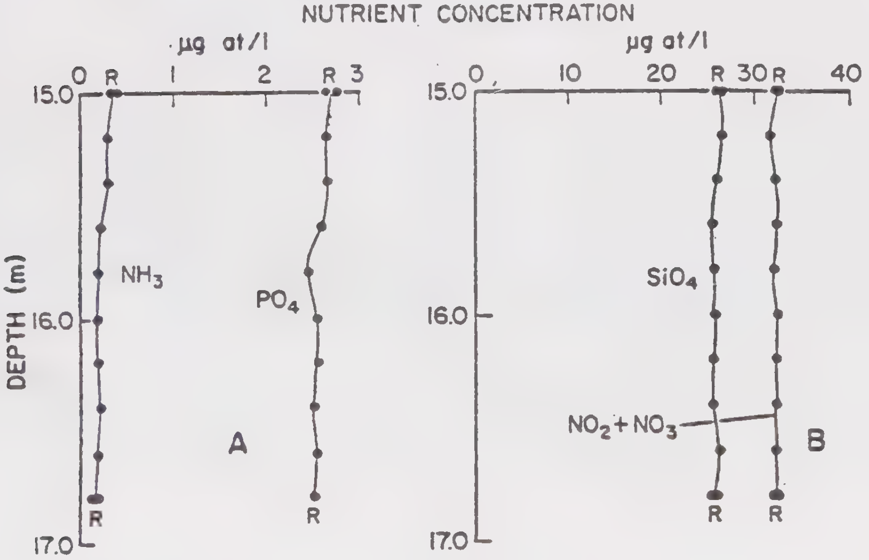

Figure 5. Microscale variation of nutrient salts in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

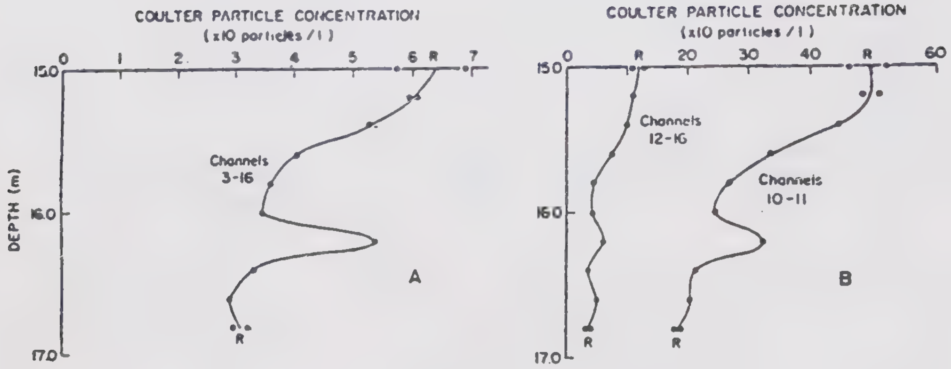

Figure 6. Microscale variation of particle counts (Coulter TA) in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

Despite the dynamic conditions encountered, microstructure of the several organisms was at least as pronounced in the "mixed layer" near Peru's shelf-break as in the more stable layer at the same depth near the coast. None of the variations were in the form of stepped trends but were all of sub-metre extent (Fig. 7). Small ciliates (20-50 μm) were less numerous and covaried with the small ciliates.

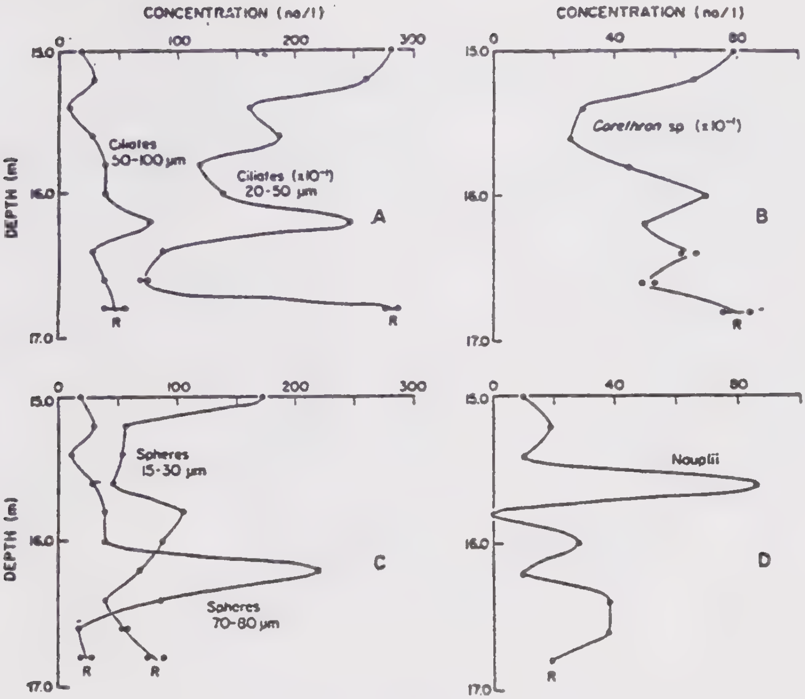

Figure 7. Microscale variation of larval anchovy food and non-food organisms off Peru's shelf-break in November 1977 (7711/KPS-2).

Covariation with ciliates of 70-80 μm sphere concentrations indicates that ciliates had actively associated with copepod eggs in the stratum between 16.0 and 16.6 m or alternatively that these spheres were actually ciliates (an artifact of sample preservation). The former seems more likely, as the spheres were quite smooth and regular in shape, and of nearly uniform size.

Copepod nauplii, also food items, exhibited large vertical variation and close replication. A pronounced maximum of their concentration was detected 60 cm above the presumed "egg" maximum, and 20 cm above a sample containing no nauplii.

Microscale variation of nutrients was greater at the slope station than at the coastal station, despite the difference in layer stability (Fig. 8). Nutrients were lower than at the coastal station but not limiting to phytoplankton growth. Microscale variation was not as pronounced as in the SC Bight, but was detectable for silicate (which covaried with the diatom *Corethron*) and perhaps for ammonia and phosphate. Nitrite-nitrate was constant over the 2 m interval.

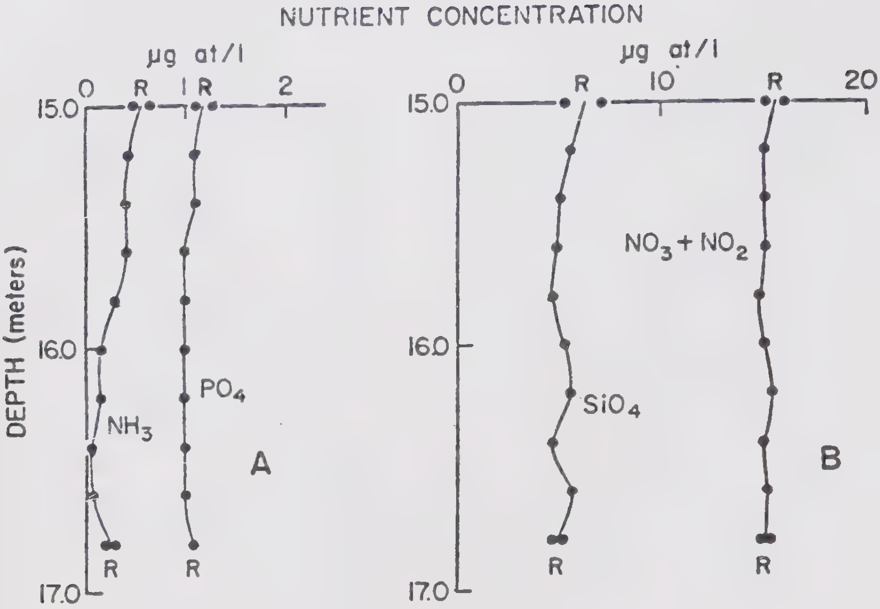

Figure 8. Microscale variation of nutrient salts off Peru's shelf-break in November 1977 (MPS-2).

Particle concentration counts from Coulter Counter was lower and less variable with depth than at the coastal station, except for the 16-50 μm category, which also showed variation on the 5 cm scale (Fig. 9). Chlorophyll a and phaeopigments, by contrast with Fig. 5, varied reciprocally with depth (Fig. 10) indicating either physical control by fine-scale lateral interleafing or biological control by localized grazing. No particular correspondence is evident between plant pigment concentration and variation of the population enumerated.

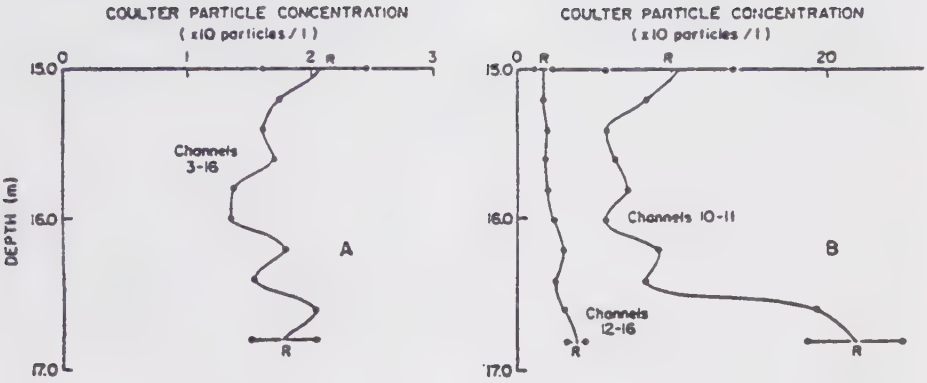

Figure 9. Microscale variation of particle counts (Coulter TA) off Peru's shelf-break in November 1977 (7711/MPS-2).

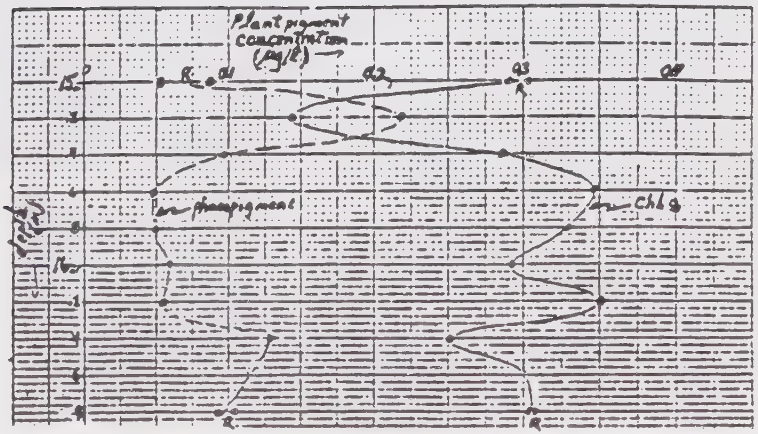

Figure 10. Microscale variation of phytoplankton pigment concentration off Peru's shelf-break in November 1977 (7711/MPS-2).

DISCUSSION

Association of plankton and biologically active substances with macroscopic flocs ("marine snow") has been reported and represents micro-distribution on the sub-cm scale. This work is of interest because it suggests yet another dimension to the complex ecological structure of the mixed layer and thermocline, e.g. organisms residing on marine snow are not available to the same predators or grazers as free-living individuals. The seaward extent of influence of marine snow is not known. My work indicates the presence of flocs affected concentrations of ciliates and detritus within 1 to 2 km of the coast but not beyond. This is confirmed by the lower incidence of aggregates in water of recent offshore origin than in neritic water, as reported by Trent *et al.* (1978).

Yet to be determined is the extent to which physical mixing mediates the microstructuring process. Dye studies by Kullenberg (1974) and Woods (1968) conducted elsewhere in density-stratified waters, show that layers of sub-metre thickness scale can persis for at least a day in the absence of storm-force winds and that disruptive processes can operate on the same scale. Only broad agreement was found during this study between degree of microstructure and estimates of vertical diffusivity from current shear and density stratification spanning layers in which microstructure was measured off California. The current meters, however, were separated vertically by 20 m. It is likely that any important mixing processes occurred on smaller scales.

The micro structure sample data suggest that small planktonic organisms overcome dispersive processes such as diffusive mixing to a degree sufficient to form laminae on the cm scale. Their vertical variation is pronounced in density-stratified water but detectable in the mixed layer as well. By water movement, reproductive rate and behaviour, plankton become differentially layered in what may prove to be microniches. The existence of the microniche is indicated in my work by the accompanying cm-scale variation of non-living particulates and of nutrient salts, particularly that of nitrogenous nutrients, which are commonly limiting to phytoplankton growth in these waters. Spatial partitioning of microplankton populations likely increases the capacity of the habitat to support greater community diversity and higher standing stocks because interspecific competition for resources is reduced, in much the same fashion as in terrestrial communities. Unlike terrestrial communities, however, such partitioning in the sea is inherently less stable on the short term. As examples, increased mixing during wind storms would modify if not destroy fine-scale variation, and the nearly synchronous diel reproduction (at times depending on species) of diatom and dinoflagellate populations likely produces daily changes in plankton microstructure. How such processes of mixing and restructuring of layers affect development and evolution of plankton communities is a topic of considerable interest.

It now appears that niches for plankton organisms may identifiably occur in midwater on a variety of spatial scales. For example, Reid *et al.* (1978) were able to distinguish between coastal phytoplankton communities of the upper mixed layer and the density-stratified layer from larger scale, vertically integrative pump samples, and below the sub-metre niche proposed here is the sub-centimetre niche created by marine snow for both phytoplankton and small zooplankton, as identified by Alldredge (1972) and by Silver *et al.* (1978).

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A DIRECT METHOD FOR ESTIMATING NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SPAWNING BIOMASS

Two methods exist for estimating spawning biomass, the total weight of mature fish, from abundance of spawning products. The first, or direct, method (Saville 1963) consists of dividing an estimate of egg production by the product of batch fecundity and the proportion of females in the mature stock. Saville safely assumed spawning frequency to be unity. The second method is indirect (Murphy 1966; Smith 1972) and utilizes information from two different species. Smith illustrated the second method, using information on the Pacific sardine, *Sardinops caerulea*, and northern anchovy, *Engraulis mordax*. Sardine spawner biomass is estimated from landings data and cohort analysis; anchovy spawner biomass is estimated by multiplying the estimated sardine spawner biomass by the product of the anchovy-to-sardine ratio of larval abundance and the sardine-to-anchovy ratios of fecundity, and spawning frequency. Computation was facilitated by assuming the unknown spawning frequencies to be equal, making the ratio of spawning frequencies unity. Up to the present only the second method has been used for the northern anchovy. This paper presents estimates derived from the first.

Computation of spawning biomass is simplified for the direct method when spawning occurs but once and for the indirect method when both species spawn with equal frequency. Difficulties arise when spawning is continuous and when it cannot be safely assumed that all mature fish spawn with the same frequency. This is the case with the northern anchovy. Spawning products are present all year, with a maximum abundance occurring in the late winter and early spring and a minimum during late summer and early fall. Abundance of and seasonal pattern of spawning products give no clue as to the number of spawnings by size and age, or even to the average number of spawnings.

Under the following conditions spawning frequency can be estimated from examining the spawning condition of females: 1) females can be examined for a characteristic that indicates when spawning takes place; 2) the length of time such a characteristic remains detectable can be estimated; 3) the spawning rate remains relatively constant over the sampling interval.

The spawning fraction, or frequency, is the fraction of females displaying the characteristic divided by the length of the time interval the characteristic remains detectable. Say, from a sample of 10 females, 2 display a characteristic which lasts for 1 day and which indicates that spawning will take place in approximately 1 wk. The daily spawning fraction 1 wk hence will be 1/5.

Given this method for estimating spawning fraction the following relationship holds:

$$P = S(abc) \qquad (1)$$

where P = production in eggs,
a = batch fecundity in (eggs)/(unit weight),
b = fraction spawning (weight of spawning females)/(weight of all mature females),
c = (weight of females)/(weight of spawning stock),
S = spawning biomass.

Spawning biomass can be estimated directly:

$$S = P(abc)^{-1}. \qquad (2)$$

Hunter and Goldberg (1979) examined female northern anchovies for characteristics that would indicate a recent spawning. They found that following spawning follicles of the northern anchovy go through a sequence of identifiable degenerative stages. The first two stages, which Hunter and Goldberg referred to as day 0 and day 1, have durations of 1 day. Stage identification is subject to error. Day-0 follicles can be misidentified as day 1; day-1 follicles can be misidentified as day 2 and beyond. The most easily identified stage is day 1. If the spawning fraction, b, is based on day-1 follicles an adjustment factor, say d, is required in Equation (2):

$$S = P(ab'c)^{-1}d \qquad (3)$$

where b', replacing b, is the observed fraction.

The adjustment factor is computed by using information on the fraction of day-0 follicles misclassified as day 1, say d_0, and the fraction of day-1 follicles correctly classified, say d_1.

$$\begin{aligned} d &= (d_0 + d_1) \\ \mathrm{Var}(d) &= \mathrm{Var}(d_0) + \mathrm{Var}(d_1). \end{aligned}$$

Estimates based on Hunter and Goldberg's (1979, table 1) blind classification study for d_0 and d_1 are 5/21 and 16/19 respectively; hence

$$\begin{aligned} d &= 1.080 \\ \mathrm{Var}(d) &= 0.016. \end{aligned}$$

From examination of 195 females taken by midwater trawl during the time interval 15-27 February 1978, Hunter and Goldberg estimated the observed daily spawning fraction and its variance:

$$\begin{aligned} b' &= 0.159 \\ \mathrm{Var}(b') &= 4.561 \times 10^{-4}. \end{aligned}$$

Based on the total female weight of nonspawners the estimated batch fecundity and variance are from Hunter and Goldberg (1979, table 6)

$$\begin{aligned} a &= 396 \text{ eggs/g (or } 3.96 \times 10^{8} \text{ eggs/t)} \\ \mathrm{Var}(a) &= 886. \end{aligned}$$

For the time period 18 February-17 March 1978, Zweifel[1] estimated daily egg production. From 177 plankton samples, northern anchovy eggs and larvae were staged from time of spawning. Estimated total numbers at stage were regressed on time. The ordinate intercept, number at time zero, is the estimated egg production:

$$\begin{aligned} P &= 2.321 \times 10^{13} \text{ eggs/d} \\ \mathrm{Var}(P) &= 1.825 \times 10^{26}. \end{aligned}$$

If the female to male sex ratio in numbers were 1:1 and if the two sexes had equal growth rates in terms of weight then c could be assumed to be 0.5. However, because of conflicting and insufficient evidence neither of these two hypotheses can be supported. Klingbeil (1978) demonstrated that the distribution of northern anchovy sexes is heterogeneous over space and time and that estimates of sex ratio are dependent on the sampling gear. From the purse seine fishery Klingbeil estimated that the ratio of numbers of females to males varies between 1.14:1 and 2.02:1 for 1969-76. From 9 yr of midwater trawl data Klingbeil estimated that the sex ratio is 1.03:1. Since midwater trawl surveys cover a wider geographic area and size range of anchovies, they probably provide an estimate closer to that of the true population sex ratio. However, since neither midwater trawl surveys nor purse seines are designed to estimate sex ratio it can only be stated that the anchovy sex ratio has not been adequately estimated.

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[1] James Zweifel, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.

Collins (1969) showed that females are greater in length and weight at age than males. However, since Collins' estimates are based on combined data from three fishing seasons and, since female weights are known to fluctuate within season due to spawning activity, the precision with which the data can be used for estimation purposes is open to speculation.

For the present purpose of estimating c the sex ratio of the number of females to males plus females as estimated from the February 1978 midwater trawl survey (Hunter and Goldberg 1979) will be used. Reexamining original data used by Hunter and Goldberg (1979, table 5) the ratio estimate is

$$\begin{aligned} c &= 0.550 \\ \mathrm{Var}(c) &= 0.001. \end{aligned}$$

This assumes, of course, an equal weight at age.

In the future, the best estimate of c is likely to be the ratio of the actual sampled weights of males and females; these were not available for the February 1978 survey. This would, of course, require the assumption that the sex ratio can differ from 1:1, that the weight distribution of the two sexes can change with time, and that a sample estimate is a better estimate than any hypothesized or long-term average value.

Using the following estimates

$$\begin{aligned} P &= 2.321 \times 10^{13}\ \text{eggs/d} & c &= 0.550 \\ a &= 3.96 \times 10^{8}\ \text{eggs/t} & d &= 1.080 \\ b' &= 0.159 \end{aligned}$$

the estimated S is approximately 0.72 million t. This is reasonably close to the estimate by the Smith procedure (Stauffer and Parker[2]) of 1.17 t.

At this time caution should be exercised in interpreting the general range described by these two estimates. The parameters of Smith's procedure have not been formally estimated. The parameter estimates of this new method are only first approximations. P may not be constant for as long a time interval as assumed here. Observed b' was found to be consistent for time of day, weight of fish, and geographic location. This may not prove to be the case under more intensive sampling. Another problem in estimating the spawning fraction is in determining female sexual maturity. This problem may be particularly acute for recently spawned young females where microscopic analysis is necessary to separate the recently spawned from the sexually immature. Misclassifying recently spawned as immature would tend to inflate the estimated b.

By the delta method (Seber 1973), the variance of S is

$$\mathrm{Var}(S) = (ab'c)^{-2}\left[d^2\mathrm{Var}(P) + P^2\mathrm{Var}(d) + (Pd)^2\left[\frac{\mathrm{Var}(a)}{a^2} + \frac{\mathrm{Var}(b')}{b'^2} + \frac{\mathrm{Var}(c)}{C^2} \right]\right]. \quad (4)$$

Dividing Equation (4) by the square of Equation (3) and then taking the square root we have the coefficient of variation (CV) of spawning biomass

$$\mathrm{CV}(S) = \sqrt{[\mathrm{CV}(P)]^2 + [\mathrm{CV}(a)]^2 + [\mathrm{CV}(b)]^2 + [\mathrm{CV}(c)]^2 + [\mathrm{CV}(d)]^2}, \quad (5)$$

which is the component vector of the coefficients of variation of the estimated parameters, right side of Equation (3). Since possible covariance terms are neglected, Equation (5) may be somewhat oversimplified. However, Equation (5) allows a first approximation to delegating the relative impact of the precision of the individual parameter estimates. The squared coefficients of variation are as follows:

$$\begin{aligned} [\mathrm{CV}(P)]^2 &= 0.339 & [\mathrm{CV}(c)]^2 &= 0.003 \\ [\mathrm{CV}(a)]^2 &= 0.005 & [\mathrm{CV}(d)]^2 &= 0.013. \\ [\mathrm{CV}(b)]^2 &= 0.018 \end{aligned}$$

Thus $\mathrm{CV}(S) = 0.614$. P contributes approximately 8 times more to the coefficient of variation of the spawner biomass estimate than all other parameters combined. In the future, additional effort will be allocated to estimating production.

The utility of the direct method, Equation (2), lies in the fact that all the parameters can be estimated. The same samples used for estimating b' can be used to estimate a and c. This can be done with 2 wk of midwater trawling. It is hoped that precise estimation of production can be done within 30 d by sampling for eggs; this goal seems attainable for the northern anchovy. Utilization of the method for other species seems feasible.

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[2] Stauffer, G. S., and K. R. Parker. 1978. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1978-79 fishing season. U.S. Dep. Commer., NOAA, NMFS/SWFC Adm. Rep. LJ-78-9, 10 p.

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these problems and because the estimation from 1968–79 was based upon extrapolation with fixed parameters that:

(a) an underlying predictive model of the dynamics should be developed on the basis of data in Area VI and other Southern Hemisphere fin whale stocks.
(b) evidence from sightings data should be carefully analysed
(c) recruitment rates from age structures should be analysed

before any recommendation about a change in management status could be made.

Other members believed the present result confirmed the reliability of the previous assessment by Chapman (1976) on the population of the fin whales in Area VI. They considered that monitoring of the stock by sightings data (SC/31/Doc 4) also proved it. The stock was estimated to have recovered to 93.5% of the MSYL in 1979/80 according to SC/31/Doc 34. Therefore, these members recommended that the fin whale stock in Area VI should be reclassified as SMS with a catch limit of 156 for the 1979/80 season, based on the present management scheme.

Re-opening of the exploitation will be expected to provide much data and materials to develop the needed information for the population assessment.

Research catches

Some members felt that at this stage a research catch would be premature for all the reasons given above. Holt referred to the criteria for any take of substantial numbers of whales under special permits contained in his minority statement (*Rep. int. Whal. Commn* 20: 42) and expressed his view that such criteria had not yet been satisfied.

Other members stressed that there is urgent need for collection of parameter value information by research catches to resolve the problems associated with the present uncertainties of the analyses.

Annex I

REPORT OF THE SUB-COMMITTEE ON SMALL CETACEANS

1. PARTICIPANTS, AGENDA AND INTRODUCTORY REMARKS

Members (M) of the Standing Sub-Committee or the Scientific Committee of the IWC, invited experts (E), and observers (O) attending the meeting were:

Allen, R. (E), Berney (O), Best (M), Braham (M), Brownell (M), Cameron (E), Christensen (M), Davis (E), Gong (M), Goodall (E), Jonsgård (M), Kapel (M), Kelly (O), Kemper (E), Klinowska (M), Lomax (M), Marcet Ocaña (M), Mitchell (M), Perrin (M, Chairman), Rørvik (M), Rudge (M), Saito (M), Sergeant (E), Suda (M), Wada (M).

All participants did not attend all sessions of the meeting.

The draft agenda was discussed and approved with minor modifications (Appendix 1). Several of the participants had not been involved in previous meetings of the sub-committee and they requested information on the mandate of IWC concerning small cetaceans. The Chairman provided a summary of main small cetacean actions during 1976–78 (Appendix 2).

Rapporteurs for the sub-committee meeting were Sergeant (agenda items 1–4 and 9), Goodall (item 5), Davis (6), R. Allen (7) and Kemper (8).

2. DOCUMENTATION

Documents available to the sub-committee and containing information on small cetaceans were SC/31/Prog Reps 1–12 (not 7); SC/31/SM1–SM23; SC/31/Docs 15, 25 and 51; and the provisional issue LXXXIII of International Whaling Statistics.

3. REVIEW OF MANAGEMENT ACTIONS AND RESEARCH ON NORTHERN BOTTLENOSE WHALE, STRIPED DOLPHIN, DALL'S PORPOISE AND HARBOUR PORPOISE

3.1 Following a comprehensive review of the biology of the fisheries for smaller cetaceans in Montreal, April 1974 (E. D. Mitchell, ed.; *J. Fish. Res. Bd. Can.* Vol. 32 No. 7), the 28th Annual Meeting of the Commission concluded that all cetaceans taken for their own value (i.e. direct takes) be subject to consideration by the Scientific Committee and that the following species in the following areas should be considered for immediate action:

(1) northern bottlenose whale *(Hyperoodon ampullatus)*, North Atlantic;
(2) striped dolphin *(Stenella coeruleoalba)*, North West Pacific;
(3) Dall's porpoise *(Phocoenoides dalli)*, North West Pacific; and
(4) harbour porpoise *(Phocoena phocoena)*, North Atlantic.

At the 27th, 28th and 29th Annual Meetings, the Commission agreed with the Scientific Committee's recommendation that the Secretariat and governments of member nations be urged to initiate or augment research on species involved in direct fisheries. These included recommendations on the above species as outlined in the sub-committee's 1976 report *(Rep. int. Whal. Commn* 27: 481).

3.2 New Information

3.2.1 Northern bottlenose whale, North Atlantic

This species was provisionally listed as a Protection Stock for the entire North Atlantic in 1978 and 1979, pending the accumulation of sufficient information for classification. The sub-committee notes that the bottlenose whale research program recommended in 1977–79 was not carried out this year, as reported by Jonsgård. The Norwegian fishery for bottlenose whale has ceased and no new data were available on stocks. The sub-committee continues to request and recommend that this program be carried out as recommended at the 1977 meeting *(Rep. int. Whal. Commn* 28: 66). The sub-committee also recommends that the provisional classification as a Protected Stock should remain (see Recommendations to the Scientific Committee). Attention was drawn to a recent review of the biology of the species (Benjaminsen and Christensen, 1979).

3.2.2 Striped dolphin, northwest Pacific

This species is subject to a direct fishery by the drive-in method in Japan. Although extensive biological and population studies had been carried out, several specific research needs were identified in 1976 (Report of Small Cetaceans Sub-Committee, *Rep. int. Whal. Commn* 27: 481). These included catch and effort statistics by species; tagging and census studies to obtain information on school structure, migration, and definition of stocks; and monitoring of life history parameters. Some of these have been accomplished.

While the sub-committee recognises the problems involved in gathering catch and effort data by species in mixed-species fisheries, the sub-committee strongly recommends that a research program to gather these data be expanded as soon as possible (Appendix 6). The sub-committee notes that Japan is implementing such a program.

3.2.3 Dall's porpoise, northwest Pacific

This species is involved in both direct and incidental fisheries. The sub-committee notes the initiation of co-operative research by the USA and Japan (SC/31/Prog Rep 6) and recommends that this research be continued and augmented if possible (see also 5.1.5).

Precise statistics on the directed take in the shore-based fishery in Japan are desired.

Suda reported that the Japanese Fisheries Agency has begun a program of research on the harpoon fishery for Dall's porpoise on the northeastern coast of Honshu. The program will include collection of detailed catch statistics, collection and analysis of biological samples, and studies of population size and status (Appendix 6).

3.2.4 Harbour porpoise, North Atlantic

This species is involved in both direct and incidental fisheries. No reliable estimates of recent takes by the USA and Canada are available. The direct and incidental fisheries along the west coast of Greenland have resulted in annual takes of up to 2,500 porpoises in recent years; approximately 700 animals were taken in the direct fishery in 1978 (SC/31/ProgRep 43. Because the harbour porpoise is a coastal species, the catch must be considered substantial for such a restricted area.

An aboriginal fishery for the harbour porpoise initially pursued by Indians of the Passamaquoddy and Micmac tribes in the Bay of Fundy and Grand Manan Island (summary and references in Mitchell, 1975b: 95, 97) may still exist. The US and Canadian progress reports do not contain statistics for this fishery. D. E. Gaskin and co-workers, University of Guelph in Canada, continue research on harbour porpoise biology, based on samples and observations in the Gulf of Maine, Bay of Fundy and Passamaquoddy Bay.

4. OTHER DIRECTED CATCHES OF SMALL CETACEANS

The sub-committee had available to it new information on research, management and catches of other species taken in directed fisheries, from data in documents submitted to the meeting from participants.

4.1 Japan and Korea coastal fisheries

Suda reported on a new research and management scheme for coastal Japanese waters (Appendix 6). Research is in progress on coastal fisheries for dolphins, and results will be reported later. Aggregate statistics only are available, from the Fisheries Agency (SC/31/ProgRep 6), but Suda stated that the use of varied names for the same species in different prefectures makes tabulation of statistics difficult. The Far Seas Fisheries Research Laboratory is compiling a lexicon of these names.

In the Republic of Korea, a similar problem exists in that coastal catches occur of unknown species and knowledge of local names is lacking.

4.2 Species accounts

4.2.1 Narwhal

The total take of narwhals by Greenland in 1978 was 404, excluding the Thule region. The estimated total was 550 (SC/31/ProgRep 4). Canada (SC/31/ProgRep 3) reported that the Inuit in the Canadian Arctic took 279 narwhals in 1978.

4.2.2 White whale

A take of 979 white whales was reported for Canada (406 in SC/31/ProgRep 3, plus 572—Appendix 3), taken by the Inuit. These figures include takes in Hudson and James Bays. Denmark (SC/31/ProgRep 4) reported a known take of 387 white whales with an overall estimate of 500 to account for lack of information from the Thule area.

4.2.3 Killer whale

In Norway, 54 killer whales were taken under license subsidy by the government (see 5.2).

Canada (SC/31/ProgRep 3) reported a catch of one killer whale.

Ivashin (USSR) reported (through Sergeant) that catches of killer whales by Soviet whaling vessels in the Antarctic were 77 in 1978 and 49 in the early 1979 season. The whale carcases are processed for oil and animal food. Full suites of biological data and specimens are collected from the whales. Catches over the last 10 years (1969–78) have ranged from 2 (1970) to 77 (1978). Adequate assessments of the stocks being fished have not been carried out. (SC/31/Doc 25, Figs. 5 a–b) recorded, without comment, sightings of numbers of large killer whales in Areas IV W and IV E (total ≳700). These data indicate that killer whales are widespread and abundant in these areas. None the less, the sub-committee believes that this fishery should be pursued only provisionally, pending stock assessment.

4.2.4 Pilot whales

The take of long-finned pilot whales, *Globicephala melaena*, in SW Greenland was 97 in 1978 and 71 in 1977 (SC/31/ProgRep 4).

The United Kingdom (SC/31/ProgRep 11) was unable to give any figures for the St Vincent Islands, but in 1978 three 25 foot boats, each manned with a crew of six, hunted pilot whales with harpoon guns from January to November. Eleven pilot whales were taken in Japan in 1978.

4.2.5 White-beaked dolphins

This species is taken off Labrador for local consumption (SC/31/ProgRep 3).

One dolphin, *Lagenorhynchus* sp., and three other unidentified small cetaceans were caught off SW Greenland (SC/31/ProgRep 4).

4.2.6 Peale's dolphin

Goodall reported that 23 Peale's dolphins, *Lagenorhynchus australis,* were captured for bait for *centolla* traps in southern Argentina in 1978, a take which has since stopped.

In southern Chile (Magallanes), large numbers, mainly this species and *Cephalorhynchus commersonii,* an estimated 2,350 from July 1976 to January 1977, and a similar amount in the 1977–78 season, were harpooned for *centolla* trap bait.

4.2.7 Bottlenose dolphin

This species was probably among the 20 animals taken for local human consumption near the Island of St Helena (SC/31/ProgRep 11).

Marcet Ocaña reported that until 1974 taking of dolphins, mainly *Tursiops,* along with other marine mammals and birds, took place in the Gulf of Mexico for bait for hook and line shark fishing. This is now prohibited and controlled in Mexico.

Some bottlenose dolphins may be captured by driving at Bahia Sanborombon, Argentina but no statistics are available (SC/31/SM 3).

4.2.8 Ocean dolphins

Some ocean dolphins, *Stenella,* are taken along with the pilot whale fishery in St Vincent, and are probably among the 20 animals taken annually in St Helena (SC/31/Prog Rep 11).

4.2.9 Harbour porpoise (See 3.2.4)

In 1976, (*Rep. int. Whal. Commn* 27: 510), Kapel noted that there had been a decline in the take in most recent years of *P. phocoena* in Greenland, from 1,000–15,000 to about 700–800 animals. In the late 1960's and early 1970's, the directed and incidental take may have reached 2,500 animals.

Kapel reported that some incidental capture of *P. phocoena* still occurs in the salmon fishery, but that it has decreased because few foreign vessels are presently carrying out salmon fishing in West Greenland waters. Catch statistics of directed and incidental catch are reported together, so the proportions are not known. The porpoise are used for food.

The sub-committee recommended research, documentation of effort and historical research on the West Greenland harbour porpoise. Kapel commented that this would not be possible at present because of the nature of the records and because of the limited staff and funds available for research in Greenland that would more likely be allocated for research on seals and other whale species, on which the need for studies and collection of data are considered more urgent.

Mitchell believes that on zoogeographic grounds, the West Greenland harbour porpoise is likely an isolated stock, and that the magnitude of removals in the last 10–15 years warranted concern for the status of this stock. The sub-committee then recommended a reassessment of possibilities of research on harbour porpoises in Greenland.

5. PROBLEMS OF INTERACTIONS BETWEEN FISHERIES AND SMALL CETACEANS

The sub-committee reviewed a number of documents and progress reports which dealt with this subject. These were SC/31/SM1, 3, 4, 11, 20 and SC/31/Prog Reps 1, 2, 3, 4, 5, 6, 8, 9, 10, 12. Additional information was provided by sub-committee members and invited experts.

In 1978 (*Rep. int. Whal. Commn* 29: 26–27) the Commission endorsed the recommendations of the Scientific Committee through the Technical Committee to encourage research by member nations into competition between small cetaceans and fishermen (13.4) and that statistics and data on all types of small cetacean fisheries (including direct, incidental and live capture) should be submitted to the IWC as part of the national scientific report (13.6).

The sub-committee reviewed the following new information.

5.1 Incidental takes

5.1.1 North America

Canada. Porpoises are taken in cod traps in Newfoundland, in mackerel nets in the Gulf of St Lawrence, and on the Labrador coast (refs. in Mitchell, 1975b: 95), but the sub-committee has not received any recent statistics on these incidental takes.

5.1.2 South America

Brazil. H. P. Castello (letters of 16.i and 5.ii.1979) has data on incidental killings of dolphins during beach seining operations in Rio Grande which involve 'numerous' franciscanas, *Pontoporia blainvillei.*

Uruguay. Praderi (SC/31/SM 4) reported that many franciscanas, *Pontoporia blainvillei* continue to be caught in the shark gill-net fishery off the oceanic coast of Uruguay, particularly at Punta del Diablo. The number caught in 1978 (254) was the same as in 1977, and slightly higher than in 1976 (244). He feels that because of the increasing emphasis on fishing with larger vessels farther offshore, the mortality of *P. blainvillei* is expected to decline in the future.

Argentina. Goodall (SC/31/SM 3) and Goodall and Cameron (SC/31/SM 1) reported that undetermined numbers of dolphins, mainly Peale's dolphins, *Lagenorhynchus obscurus;* bottlenose dolphins, *Tursiops truncatus,* franciscanas *Pontoporia blainvillei; Stenella* sp.; and possibly Commerson's dolphins, *Cephalorhynchus commersonii,* may be taken during fishing for *anchoita, corvina, caballa, abedejo* and other fish in the provinces of Buenos Aires, Rio Negro and Chubut, but that numbers are probably small. In Tierra del Fuego, Commerson's dolphins and others die in tangle nets used from shore for the capture of *robalo* and *merluza.* Specimens recovered were 23 in 1978 and 21 in 1977, but the number of dolphins killed was much greater; since the fishermen do not utilize them, most are discarded.

Chile. Goodall (SC/31/SM 3) reported that a considerable incidental take of Burmeister's porpoise, *Phocoena spinipinnis,* and *Cephalorhynchus eutropia,* occurs during net fishing for *congrio* and other species off the coast near Valdivia. No information on numbers is available: the dolphins are used for bait, human consumption and possibly fish meal.

Goodall also reported the incidental capture of *C. commersonii* and possibly *Lagenorhynchus australis* in *centolla* nets in the area of the Strait of Magellan. No definite statistics are available but an estimated 300 dolphins may be taken per year. This incidental take is declining with the gradual change from nets to traps for southern crab.

Peru. Valdivia reported that at present, there is no directed take of dolphins, but some unloading of incidental catch taken during purse seining for pelagic fish (*anchoveta, sardinas, caballa* and *jurel*) does occur. No statistics are available. Recently, there has been a greater demand for dolphin meat in the markets of small coastal Peruvian ports, which could be an incentive for increased retaining of dolphins.

The Instituto del Mar del Peru (IMARPE) cannot carry out its approved plans of investigation on small cetaceans at present because of limited funds, but possibly studies will begin in the near future.

5.1.3 Africa

Senegal. J. Maigret (letter to IWC, 1979) has advised that investigations have begun on the small cetaceans involved in the yellowfin tuna purse-seine fisheries, which produce the death of 'numerous dolphins'. Observation forms have been distributed and conferences with neighboring countries planned.

According to A. Fonteneau (letter to G. Sakagawa, 12.iv.1979), the fishermen do not use the dolphins on the Ivory Coast and Senegal, and the dolphin catch is probably low.

Seychelles. L. Watson reports that the Seychelles have a small incidental take (about 30 per year) of dolphins, mainly *Stenella.* Under the new Seychelles Marine Mammal Act, all catches in the future will be reported and definite data should be available by the next meeting.

South Africa. In 1978 the reported mortality was less (SC/31/ProgRep 9) than in 1976. One Heaviside's dolphin, *Cephalorhynchus heavisidii,* was trapped in a purse seine net. Forty-four dolphins were trapped in shark nets; the six of these which were examined were bottlenose dolphins, *Tursiops.*

5.1.4 Europe

Norway. E. Christensen reported that harbour porpoises, *Phocoena phocoena,* are caught incidentally in fishing nets, but that the number taken is small.

Denmark. See 3.2.4.

5.1.5 Asia

Japan. The 1979 progress report was indefinite on the number of small cetaceans caught incidentally, since both incidental and deliberate catches were included in Table 2 (SC/31/ProgRep 6). No figure was given for 1978 but 16,074 was reported for 1977 and 18,453 for 1976 for both types of take.

The USA and Japan, under the aegis of the International North Pacific Fisheries Commission, have completed the first year of a three-year study of Dall's porpoises taken in the Japanese salmon gill-net fishery. Data and specimens were collected from 354 Dall's porpoises incidentally captured within the United States' 200 mile fisheries zone off the Aleutian Islands during the summer of 1978. Preparation and analysis of ovaries, testes, stomach contents and teeth is continuing.

Sightings data were also collected aboard Japanese research vessels by US and Japanese scientists and on US vessels of opportunity. Progress reports were submitted by both countries to the Scientific sub-committee of the Ad Hoc Committee on Marine Mammals of the International North Pacific Fisheries Commission, which met in March 1979, in Tokyo.

5.1.6 Eastern Tropical Pacific (Purse-seining for tuna)

The estimated kill of dolphins and small whales in the US tuna fishery declined from 490,000 in 1970 to 27,000 in 1977 and 14,946 in 1978 (SC/31/SM 11). Figures for the first five months of 1979 totalled 10,859. The US kill has gone down in the last two years, with that for 1978 being only half as much as 1977. In 1979 there was less fishing for skipjack, so the kills have been higher. The % of captured animals has not declined, but the % of captured animals killed has declined.

SC/31/SM 20 reported that purse seining for yellowfin tuna has been carried on by Canadian vessels in the eastern tropical Pacific since the 1960s. Two-inch mesh panels were installed to prevent dolphin entanglement in 1974, 1¼in panels in 1977 and 'aprons' during 1978. The operation of vessels tended to be directed more at 'school' rather than 'on porpoise' fishing. Information from logbooks and occasional observers indicated the number of sets 'on porpoise'. Using the rates obtained on similarly operated US vessels, the estimate of dolphin kill for 1976 was 131; in 1977 it was 462 and 106 in 1978. During 1976 an observer program is being carried out in accordance with Inter-American Tuna Commission (IATTC) recommendations. Canada is participating in the IATTC observer program.

At its 33rd meeting in 1976 the IATTC agreed to concern itself with the problem of dolphins killed incidental to purse seining for yellowfin tuna in the eastern Pacific. A research program was founded last year and is now under way. This includes an observer scheme for collecting data on the abundance and incidental mortality of dolphins. In addition, the program is to include population assessment, studies of dolphin biology and gear research.

1979 will be the first year for which there will be estimates of kills for the entire international purse seine fleet, and these will be reported next year.

Other IWC nations known to participate in the purse-seine fishery for yellowfin tuna in the eastern tropical Pacific include Panama, Mexico, New Zealand and Peru. Statistics on kill of dolphins in tuna-seining operations have not been reported by these member nations.

5.2 Direct Conflicts and Competition

In 1978 the sub-committee recommended and the Scientific Committee and the Commission agreed that the Commission foster and support research by member nations into general and specific competitive relationships between small cetacean populations and fish populations, as well as providing data on kills to IWS. (*Rep. int. Whal. Commn* 29). New information was reported to the sub-committee as follows:

5.2.1 Japan

Suda reported that at Iki Island, off the coast of Nagasaki, fishing takes place for yellowtail by day and for squid at night. The islanders scatter bait to gather and feed schools of fish in the area. Dolphins and small whales, mainly *Pseudorca crassidens and Tursiops truncatus,* have moved into this region and are reported to do extensive damage by eating the bait, the hooked fish and damaging fishing gear. Suda reported that 1,000 tons of anchovy is spread over the area during a period of 200 days per year, as bait and food for the yellowtail Sometimes the dolphins drive the fish away and other times eat them. At night they eat the squid. Killer whale sounds, speed boats and other methods were tried in 1979 to frighten the dolphins, but nothing has worked. This fishery has gone on for 20 to 30 years, but the build-up of dolphins is fairly recent; Japanese scientists cannot explain the concentrations of dolphins. No study of stomach contents has been carried out to quantitatively assess the supposed consumption of bait, yellowtail and squid by the cetaceans.

Suda also reported that conflicts exist between small whales, probably *Pseudorca,* and the tuna long-line fishery over a wide area in the tropical Pacific. Sometimes two or three years pass without damage, except for sharks, but some years 'sochi', *Pseudorca* and/or other small whales damage 5% of the tuna catch, a loss to the fishermen of about $25–30,000,000. Fishermen can tell if the damage is by sharks or dolphins, as the method of biting is different.

The Japanese fishery associations have asked for research on the problems. Some data can be obtained from log books, and expanded research is planned (Appendix 6).

5.2.2 India

A letter from a reporter for the Times of India (Shailendra Ghorpade to E. Mitchell, 1 July 1978) stated that a bounty was being paid by Maharashtra State to local fishermen for the killing of porpoises. No information was given on the species, reason for the bounty or numbers involved.

5.2.3 Norway

Christensen reported Norway has been taking killer whales inshore since 1976 under licence and with a subsidy from the Norwegian government. The take in a small-type-whaling operation has the purpose of controlling perceived competition by killer whales with herring fishermen for inshore herring stocks. The herring stocks in offshore waters have been much reduced and those populations left are now concentrated near fiords and are vulnerable to killer whale predation.

The sub-committee noted that this fishery constitutes a resumption of a fishery which almost died out in the early 1970s. Inshore catches for the last ten years have been: 1969—189, 1970—232, 1971—18, 1972—7, 1973—1, 1974—6, 1975—2, 1976—0, 1977—7 and 1978—54; ten year average is 52 whales (IWS and Prov. issue LXXXIII).

Christensen is monitoring the catch, collecting teeth and ovaries through a reward system to the whalers. The blubber is rendered to oil, and the meat is used by fox farms. Animals sampled to date have been very fat and females have a high pregnancy rate. No estimates of size of population(s) or status of stock(s) have been made.

5.2.4 Gulf of Guinea

At the November, 1978 meeting of the International Commission for Conservation of Atlantic Tunas (ICCAT), potential conflicts between 'killer whales' and tuna fishing in the Gulf of Guinea were reported. Dumping at sea of undersized yellow-fin tuna has attracted killer whales, which eat these fish and have begun to follow vessels even when not dumping, or surrounding them when stationary. There is fear that the population of killer whales will build up and that they will disperse schools of live fish by attack or tear nets to obtain the fish (Kume, 1978; Kwei and Mensah, 1978). The sub-committee urges Japan to collect data on species, numbers and behavior of cetaceans involved in the fishery and quantitative estimates of tons of tuna discarded and eaten by the whales.

5.2.5 Canada

The increasing problem of cetacean encounters with fishermen's nets in Newfoundland has prompted a research program by government and university scientists (J. Lieu, Memorial Univ.) on the subject (SC/31/ProgRep 3).

5.2.6 Mexico

Marcet Ocaña reported that Mexico has begun a program of research on marine mammal/fishery conflicts. The first work concerns problems with California sealions, *Zalophus californianus,* but cetacean problems will also be researched.

6. EFFECTS OF POLLUTION AND INDUSTRIAL DEVELOPMENT

The sub-committee reviewed the many large industrial developments being undertaken and planned for the North American Arctic and discussed the potential effects of these projects on white whale and narwhal populations. The sub-committee also reviewed industrial and pollution problems in European waters and the special problem of decline in apparent abundance of the harbour porpoise, *Phocoena phocoena,* in the North and Baltic Seas.

6.1 North American Arctic

6.1.1 Hydro-electric Projects

Two major hydro-electric projects are underway on the large rivers draining into Hudson Bay, Canada. The James Bay project is damming several large rivers and diverting several others. The project will have major effects on the coastal marine ecology and may affect the few hundred white whales along the SE coast of Hudson Bay. Of more concern is the Nelson River Project along the SW coast of Hudson Bay. This project involves dams on the Nelson River, which drains over 1,000,000 km^2 of central Canada. In addition, the main flow of the Churchill River will be diverted into the Nelson River. The estuaries of these two rivers comprise two of three main estuaries used by calving white whales in summer. Control of the flow of the Nelson River will reduce spring flooding and delay ice break-up in the estuary, and diversion of the Churchill River will drastically reduce the flow of that river. The suitability of these estuaries for summering white whales could be severely reduced. The effects on the West Hudson Bay population of 5,000–10,000 white whales are unknown and are not being studied.

6.1.2 Coastal Mining Developments

Construction of heavy metal mines near sea coasts could pose a serious threat to local marine food chains. In Greenland, the Black Angel lead-zinc mine which deposits its tailings directly into the sea has resulted in a rapid rise of heavy metals in the water column and marine organisms. The fiord involved is now heavily polluted, which has resulted in the death of most organisms, and there is some evidence that the situation is spreading to the adjacent fiord (Greenland Fisheries Investigations, Annual Reports 1974–77). Kapel reported that studies of these effects are being continued; sampling includes tissues from ringed seals but not other marine mammals.

The Nanisivik mine (Baffin Island, Canada), also a lead-zinc mine, is depositing its tailings into a lake which overflows into the sea. Background levels of lead, zinc, cadmium, and mercury were high in local organisms, including narwhal, before the mine developed. Kemper reports that some evidence suggests that cadmium biomagnification has occurred in the food chain and levels are very high in narwhal brain tissue. Since resident seals, char and narwhal are used for human food, monitoring programs must precede and parallel such developments. A monitoring program is planned for August 1979.

6.1.3 Oil and Gas Exploration

A large amount of exploratory drilling is underway and planned in offshore regions of the North American Arctic. Drilling in these areas is extremely costly and environmentally hazardous because of severe ice conditions. Drilling in Arctic regions usually occurs during the summer when the 'ice whales' (bowhead, white whale and narwhal) are present in these areas. The principal concern is that an uncontrolled blowout of oil could occur and ice conditions could prevent control of the blowout by drilling a 'relief well' for at least a year. The sub-committee is concerned that there are no reliable data on the ability of cetaceans to detect and avoid a surface oil slick. Similarly, there appears to be no information on the lethal and sublethal effects of exposure to oil on cetaceans. Thus, the effects of a major oil blowout in Arctic waters cannot be evaluated.

Exploratory drilling is currently underway in the Canadian and American sectors of the Beaufort Sea using drill-ships in offshore waters and artificial and natural islands in coastal waters. Loss of control has occurred in 3 of 12 wells drilled to date in Canada but the flow in each case was water and/or gas rather than oil. Hearings examining the desirability of increased drilling in waters along the Alaskan Beaufort Sea coast have recently been held and additional drilling in this area could begin as early as 1980. The sub-committee notes that the autumn migration routes of bowheads and white whales in the Beaufort Sea are unknown and that drilling is underway or planned for areas probably used by these whales. The sub-committee also notes that the current summer feeding grounds of the bowhead are presumed to be in Amundsen Gulf based on old (before 1910) whaling records but that no recent surveys have been conducted to verify this. The oil industry plans to drill in this area in the near future and the sub-committee believes that surveys of the numbers and distribution of bowheads on these summering grounds should be conducted.

Drilling was conducted off the west coast of Greenland in 1976 and 1977. However, the exploration was unsuccessful and has been abandoned. Offshore drilling in deep water will begin in Canadian waters in Davis Strait in 1979 and is planned for Lancaster Sound and northwest Baffin Bay. Blowouts from any of these proposed exploration or future production wells could affect major stocks of narwhals and white whales and the remnant Davis Strait stock of bowheads.

Noise, vessel traffic and other activities associated with offshore drilling could cause some disturbance and localized avoidance behaviour by whales but recent studies in the Canadian Beaufort Sea suggest that whales react only when within 1 or 2 km of a stationary source of disturbance (Fraker, 1978). Thus, direct disturbance of whales would only be a serious problem if it occurred in a major concentration area. No such activities are planned nor are they likely to be permitted by either the US or Canadian governments.

6.1.4 Shipping

Current levels of shipping activity in the North American Arctic are comparatively low but they are increasing. Studies of the effects of low levels of large traffic in the Mackenzie River estuary (Canada) indicate that white whales swim rapidly away from moving vessels within about 2 km^2 (Fraker, 1978). The effects of the high levels of traffic that would be associated with future oil production have not been studied. Sergeant (1973) has suggested that there may have been a decline in use of the Churchill River estuary by white whales since a port was established there in the 1930s.

There are several plans for construction of very large ice-breaking tankers to transport oil (if found) and liquid natural gas (LNG) from the Canadian Arctic to southern markets. The most advanced project involves plans for two 150,000 ton (ice Class 10; 150,000 horse power) LNG carriers to travel year round between Melville Island in the western Canadian High Arctic and south-eastern Canada. The ships would be involved in ice-breaking on most voyages and concern has been expressed that white whales and narwhals could follow the tracks through the ice and become trapped when the track freezes behind them. Concern has also been expressed that because the vessels will travel along the west coast of Greenland that they will interfere with the subsistence hunting by more than 4,000 inhabitants of NW. Greenland, and possibly also interfere with the wintering and migrations of narwhals and white whales. The sub-committee does not believe that there is enough information with which to evaluate the effects of this and other projects involving large ice-breaking tankers on populations of white whales and narwhals and it is important that these kinds of problems be investigated before such projects begin.

6.1.5 Marine Pipelines

Pipelines associated with the production and transportation of natural gas are planned for the Canadian Arctic. These projects involve laying of pipelines on the sea-bottom but they are not expected to cause problems for whales. A pipeline rupture that released natural gas into the water column would cause local disturbance but pollution would be low because most gas would bubble to the surface and dissipate into the atmosphere. Rupture of an oil pipeline is potentially more serious but no oil pipelines across marine channels are currently planned.

6.1.6 Research

A large amount of environmental research is being conducted by government and industry in association with the planning of some of the industrial activities discussed above. These studies are generally broad-scale impact assessments but they have provided useful information on white whales and narwhals in the North American Arctic. Some important gaps in knowledge have been outlined above and in other sections of this report. The sub-committee believes that research has been inadequate to provide appropriate data for management of most white whale and narwhal stocks. This research is vital because these stocks will come under increasing pressure from expanding aboriginal populations (the population of Inuit in Canada will double in 12 years) and from increasing industrial activities.

6.2 Europe

6.2.1 Industrial/pollution problems
European waters, particularly the Baltic, North Sea, English Channel, Irish Sea, Mediterranean and other inland seas suffer from pollution through industrial and agricultural activities and from heavy boat traffic, both commercial and tourist. There are no comprehensive programmes for monitoring the effects on cetaceans and no firm recent evidence on distribution, particularly of small cetaceans. A number of major accidents to oil tankers and to oil exploration installations have resulted in considerable spills in recent years. No efforts have been made to investigate effects on the cetaceans exposed to oil spills in European waters, either of the oil or of the chemicals used in dispersal.

There is an obvious need for systematic studies of the effects of oil and gas exploration on cetaceans in these waters and of the effects on cetaceans of pollution of these coastal waters through industrial and agricultural activity.

6.2.2 Harbour porpoise in European Waters
There are many reports that the harbour porpoise, *Phocoena phocoena,* had declined in abundance in European waters. Mitchell (1975a) concluded that early 'drive fisheries' in the Lille Belt and other fisheries and/or incidental by-catches in nets along the shores of Denmark, Poland and other Baltic Sea countries substantially reduced an initial population of 10–15,000 before 1945. The remaining population, of low abundance, may not have recovered or may have declined farther for a number of reasons. High levels of DDT and PCB in Baltic porpoises and high levels of PCB in porpoises from the Swedish west coast have been found (Olsson—letter to Klinowska, 1978). In seals, such levels of PCB are associated with pathological changes in the uterine tract leading to reproductive failure (Olsson, 1977). If this is true for cetaceans, the PCB pollution may have contributed to the population decline, although this is not universally agreed (Kapel—reporting ICES disc. 1976). It has also been suggested that climatic change may have played a role, particularly changes in ice cover (Lindroth, 1962; Wolk, 1969). Standing information indicates a decline on the Dutch, French and UK coasts (Mitchell, 1975b; Duguy, 1977; *Rep. int. Whal. Commn* 27: 500–01) although the reasons for this are not clear. As noted elsewhere in this report, European waters are particularly affected by industrial activity, mineral exploitation, oil spills and boat traffic. The problems of this species have been repeatedly discussed in the Marine Mammals Committee of ICES and a resolution was agreed by this Council in 1976, urging its members to collect material for analysis of contamination residues from all animals found dead. The Council of Europe has also recently identified the harbour porpoise as endangered by pollution (Smit and Wijngaarden, 1976). There is, however, no major support for efforts to investigate these matters either at national or international level. The sub-committee believes that this matter should be pursued by the Commission.

7. REVIEW OF DEFINITION AND STATUS OF STOCKS OF THE WHITE WHALE, *DELPHINAPTERUS LEUCAS*, AND THE NARWHAL, *MONODON MONOCEROS*

7.1 Increasing importance of fisheries

The investigation and documentation of the status of the stocks of these species is of considerable importance at the moment for the following reasons.

(1) The white whale is considered to be one potential alternative to the Alaskan bowhead whale *(Balaena mysticetus)* which is the object of a subsistence fishery (IWC, 1979).
(2) Some of the stocks have ranges which include the territorial waters of several nations.
(3) Several stocks may be over-exploited.

7.2 White Whale

7.2.1 Distribution, migration and definition of stocks
The sub-committee reviewed information in SC/31/SM 5, 8, 10, 12, 13, 14, 15, 16, 17 and 19. Perrin proposed a conceptual model of the distribution and migrations of white whales, with the features:

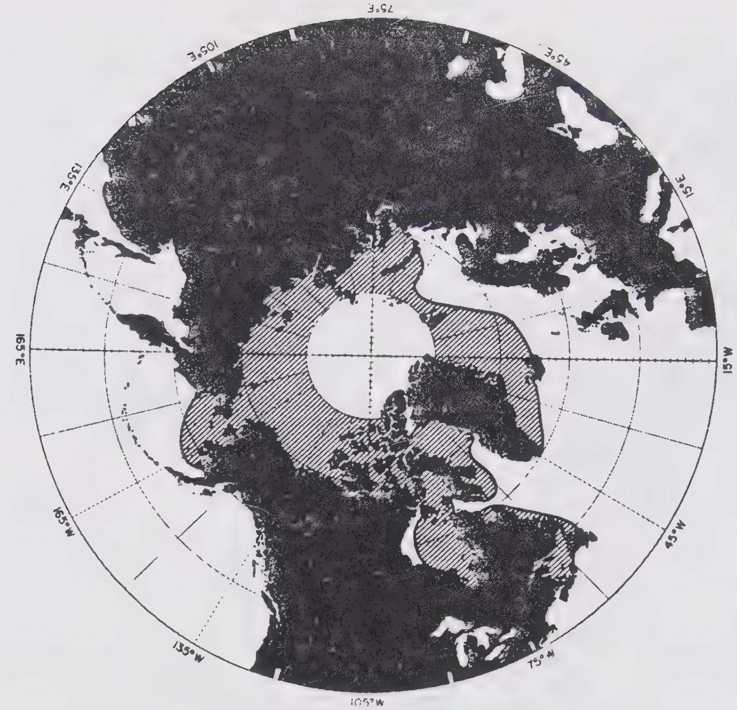
(1) Isolated year-round resident populations at low latitudes (examples: St Lawrence Estuary population and Okhotsk Sea population(s)).
(2) Several major wintering grounds near the edge of the pack ice (Fig. 1) (West Greenland, Hudson Strait, the SE. Barents Sea, and the SW. Bering Sea).
(3) Seasonal migrations of varying length to and from the small number of major wintering grounds to a much larger number of major summering grounds, typically in the region of large, relatively warm-water river deltas (examples: White Sea, mouths of Siberian Arctic rivers, Anadyr Gulf, Mackenzie River Delta, Creswell Bay in the Canadian High Arctic, and Cumberland Sound, Baffin Island).
(4) Longitudinal gaps between the ranges of the groups of high-latitude summering populations derived from the major wintering grounds, at approximately the longitudes of Iceland, the New Siberian Islands (approximately 130–150°E longitude) and Victoria Island in the Canadian Arctic (approximately 110°–120°W longitude).

The group agreed to use this model (Fig. 2) as a basis for assessing the likely degree of stock-discreteness of particular populations and that the hypothesis of wintering grounds shared by several geographical summer populations permits of two major alternative conclusions *vis-a-vis* stock discreteness, namely:

(a) wintering group consists of a single inter-breeding stock which disperses in spring, or
(b) animals in summering grounds constitute separate stocks which winter in a common area.

There was no direct evidence for either view, and it was agreed that stock assessment should be carried out considering both alternatives.

The sub-committee recognized that the model is likely an over-simplification and that minor wintering grounds exist, that year-to-year climatic variation affects the tenability of potential winter and summer grounds, and that considerable diversity of scientific opinion exists concerning the migrations and affinities of particular populations (for example, the White Sea population(s)—see SC/31/SM 13, 14 and 17).


75°E
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15°E
165°E
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135°W
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105°W

Fig. 1. Approximate limits of winter ice (15 year average).

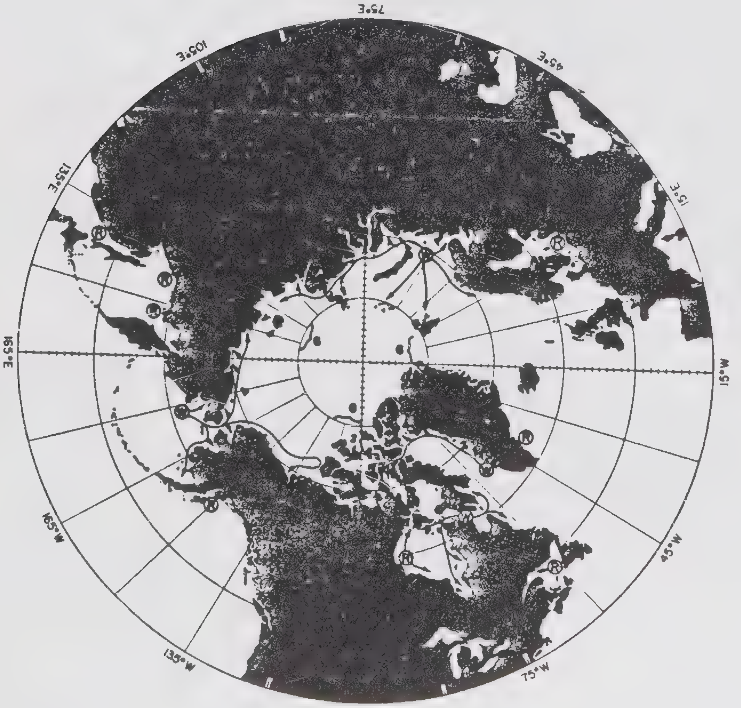
75°E
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Fig. 2. Conceptual model of distribution and movements of white whales. Arrows indicate spring migrations to main summering grounds.
W — Major wintering ground.
R — Year-round population.
G — Longitudinal gap in distribution.

7.2.2 *Age Determination and Vital Rates*

SC/31/SM 6, 7, and 15 contained information on age determination and estimation of reproductive rates.

Age determination has been based on counts of dentinal layers, and in the past the balance of opinion has been that there were two dentinal layers per year (Brodie 1967 and Sergeant 1973). However, more recent opinion, based on the same data and the analysis by Ohsumi (1979) tends to favour one layer per year (SC/31/SM 6).

The data in the table below were extracted from SC/31/SM 7 using the alternative assumptions of one or two layers per year.

	One layer/year	Two layers/year
Age of maturity, females	10 years	5 years
Age of maturity, males	16–18 years	8–9 years
Longevity	40–50 years	20–25 years
Gestation	14 months	14 months
Lactation	20–24 months	20–24 months
Frequency of calving	1 in 3 years	1 in 3 years

The data on gestation and lactation are based on direct observation and do not depend on assumptions about the rate of deposition of layers. These were based on samples from the eastern Canadian Arctic, and it was noted that a calving interval of two years had been reported for Alaskan waters (SC/31/SM 15).

Sergeant expressed the view that there is little prospect for success in estimating mortality rates from catch curves derived from teeth because of the difficulty of accurate reading of all teeth. These often exhibit irregular layering and heavy apical wear resulting in the loss of layers. The latter problem might be overcome by selection of teeth. The sub-committee feels that teeth should continue to be collected from all specimens at least in selected fisheries.

7.2.3 *Estimates of net reproductive rates*

No estimates of natural mortality rates appeared available. Therefore, the sub-committee could only review estimates of gross annual reproductive rates. Data on proportion of young-of-the-year calves in groups of sighted whales were available:

1.	Seal River, Hudson Bay	12% (Sergeant, 1973)
2.	Seal River, Hudson Bay	11.4% (Sergeant, 1973)
3.	Canadian High Arctic	11.7% (SC/31/SM 10)

Davis corrected the Canadian High Arctic estimate to 10% based on fluctuations in the proportions of immature animals present.

Sergeant (1973) calculated a gross annual birth rate of 14.3% from anatomical study of large samples of adult females. This estimate was made primarily from data for females in early pregnancy, and can be assumed to be higher then the true birthrate, as it does not take into account prenatal mortality. Brodie (1971) calculated potential instantaneous rate of increase (r) for Cumberland Sound white whales at 9%.

Based on these estimates and on rates in other small odontocetes, the sub-committee concluded that gross annual production of calves is somewhere around 10%.

The sub-committee next considered the question of whether this species exhibits density-dependent change in rates of production. Sergeant (SC/31/SM 7) compared supposedly heavily and less-heavily exploited populations. He found no change through time in average length of adult whales taken at Churchill over the period 1949–68, which, in combination with a long history of large catches, suggests to him that the West Hudson Bay population has been stable. He found no difference between the populations in mean age at attainment of sexual maturity in males and females, duration of lactation or frequency of calving.

The rest of the members of the sub-committee, however, believe that, in the absence of adequate data on effort, the assumption that the West Hudson Bay population has not experienced a change in density is not supportable. The catch declined over the period 1951–67 (Fig. 3) and the possibility exists that this was caused, at least in part, by decreased density rather than by decreased effort. The issue remains unresolved, and the sub-committee believes that additional analyses of the available data and further research based on larger samples from these and/or other populations are necessary to examine the question of density-dependent change of vital rates in this species.

7.2.4 *Estimates of population size*

The sub-committee reviewed and tabulated available population estimates for summering populations and, where available, for the major wintering grounds (Table 1). The tabulation is not complete; estimates for some Soviet populations (SC/31/SM 13), in particular are very approximate, and some of them may be missing (discussed below).

7.2.5 *Commercial and subsistence takes*

Counts and estimates of catch from a wide variety of monitoring sources were reviewed (Table 1). Kapel reported that catches on the Greenland coast are highly variable, with no clear indication of long term increase. Sergeant and Kemper reported that catch-reporting systems in Canada vary with province or territory and are non-existent in some cases. Braham reported that John Burns of the Alaska Department of Fish and Game may have estimates of white whales taken in western Alaska.

Members of the sub-committee expressed uncertainty about the reliability of the catch statistics for Ungava Bay. Roy (1971) reported that 50–60 white whales were taken annually by the Ivujivimmiut (in one village?). Davis reports having seen a processed report (Anon, 1976), which gave an annual harvest figure of 573 white whales for northern Quebec in 1975 (see Appendix 3). Sergeant expressed reservations about this catch figure. If substantiated, this would be the largest catch of white whales in Canadian waters; and if the Hudson Strait—NE Hudson Bay summer population is discrete, then no estimate of population size has ever been made of this stock. The sub-committee also notes that no statistics on this catch have been formally presented to the IWC (*cf* SC/31/ProgRep 3).

7.2.6 *Hunting loss rates*

The sub-committee notes with some concern that the losses to the hunter of whales killed or mortally wounded is a major factor in the exploitation of both the white whale and the narwhal. No systematic study of white whale loss rates has been carried out and most estimates are anecdotal, subjective and almost certainly imprecise (Appendix 4, 5; Table 1).

Table 1

Estimates of population and Harvests for major summering and wintering populations of white whale

Winter	Summer	Population estimate	Comment	Recent annual catches	% Loss rate[1]	Estimated kill No.	Estimated kill % pop'n
1. Cook Inlet, Alaska	Resident	200–500^{a}	Extrapolation of recent aerial survey	$\sim 10^{a}$	Estimated low^{b}	>10	>2–5
2. South West Bering Sea							
	a. Bristol Bay/Kuskokwim	1,000–1,500^{c}		—	—	—	—
	b. Yukon/Norton Sound	—		—	—	—	—
	c. Kotzebue Sound	—		—	67^{b}		
	d. Alaskan NW Coast	—		—	67^{b}		
	e. Mackenzie delta	4,000–5,000^{d}	Repeated recent aerial surveys	— 148 (1972–78)^{d,2} (range 123–187)	83^{b} 33^{d}	220	4–5
	f. Bering Sea (incl. Anadyr)	2,000–3,000^{e}		27 (1976–78)^{f} (range 21–32)	—	>27	1
	g. East Siberia/Chukchi Sea	1,000–2,000^{e}		None reported^{f}	—	—	—
3. Okhotsk Sea	Resident (2 populations)	6,000–10,000^{e}		None since 1969^{f}	—	—	—
4. Barents Sea		1,500–3,000^{e}		824^{3} (sum)^{f}	—	>824	>28–55
	a. Resident	—		38 (1976)^{f}	—		
	b. White Sea	500–1,000^{e}		189 (1974–77)^{f} (range 71–302)	— —	>189	>19–38
	c. Barents/Kara/Laptev Seas (several populations)	1,000–2,000^{e}		140 (1974–78)^{f} (range 19–170)	—	>140	7–14
5. St Lawrence Estuary	Resident	325^{g}	Recent ship survey	0^{4}	—	0^{4}	—
6. W. Hudson Bay	Resident	5,000–10,000^{i}	No recent survey	115 (1978)^{h}	33 (25–50)^{j}	172	2–3
7. Hudson Strait		—		323 (1975)^{k,5}	—	—	—
	a. East Hudson Bay	'few hundred'^{g}	Partial aerial survey	128 (1975)^{k}	33 (25–50)^{j}	—	—
	b. Southampton Is.	—	Possible summering area	—	—	—	—
	c. Ungava Bay	'up to 1,000^{l}'	Not based on survey	122 (1975)^{k}	33 (25–50)^{j}	—	—
	d. Frobisher Bay	250–300^{m}	Recent aerial survey	5 (1978)^{k}	—	7	3
	e. Cumberland Sound	500^{m}	Recent aerial survey	85+ (1978)^{m}	33 (25–50)^{j}	>127	>25
8. West Greenland		—		—	—	—	—
	a. Central Arctic	10,250–12,000^{n}	Recent aerial survey	11 (1978)^{6}	33 (25–50)^{j}	>14	>1
	b. Thule/Melville, or	2,000^{n}	Deduced	100^{k}	<10^{p}	110	6
	Total Management Unit	12,250–14,000	Assume a + b one stock	1,064 ($953^{7} + 11^{8} + 100^{9}$)	Various as above	1,270 ($1,146^{7} + 14^{8} + 110^{9}$)	9–10

a. SC/31/SM12
b. Appendix 5
c. SC/31/SM15
d. SC/31/SM8
e. SC/31/SM13
f. SC/31/SM17
g. SC/31/SM5
h. *Rep. int. Whal. Commn* 29: 111–14
i. Sergeant, 1973. *J. Fish. Res. Bd Can.* 30: 1,065–90
j. Extrapolated from SC/31/SM8
k. Appendix 3
l. Sergeant & Brodie, 1975
m. SC/SM/16
n. SC/SM/10
p. Appendix 4

1. Loss rate = proportion of total kill that was not landed, e.g. 33% = 1 lost for every 2 landed
2. Probably not complete
3. Including vessel take of 457
4. Possible accidental kill
5. From Hudson Strait, possibly migratory component of an unknown stock
6. Probably underestimated
7. West Greenland (south of Thule) average 1967–74^{p}
8. Canadian
9. Thule

The use of rifles rather than harpoons with fixed lines has in small cetacean fisheries necessitated a redefinition of terminology for expressing loss rates. The sub-committee proposes the following terms for future use;

Wounded-but-lost:	Animals which are non-lethally wounded and escape.
Killed-but-lost:	Animals which are mortally wounded but are not landed.

Kemper reports that loss rates are closely associated with the hunting technology (equipment) used and the situation in which the hunt occurs. Similar methods are used in the pursuit of narwhals and white whales. Fraker (SC/31/SM 18) and Brodie (1971) have documented the loss rates associated with hunts in murky river estuaries. Traditional hunting methods (SC/31/SM 16) using kayak, harpoon with floats and drogue are associated with efficient hunts characterized by low killed-but-lost rates (Durham, in IWC, 1979). The introduction of rifles, first used to kill harpooned animals and more recently employed to shoot at unharpooned quarry has greatly altered this loss rate.

Several authors have attempted to estimate sinking loss (killed-but-lost) (Table 1), but none have attempted to estimate wounded-but-lost rates, which are assumed to be much higher. In contrast to the rifle-first method used in most aboriginal fisheries, other methods are believed to be more efficient, such as the commercial drive method formerly used in Cumberland Sound, the harpoon commercial fishery in West Hudson Bay, the aboriginal and commercial fisheries using estuary-entrapment, and the Thule-West Greenland hunt, where traditional harpoon and float are still used.

Net fisheries are highly efficient (SC/31/SM 16), but are not popular with the aboriginal peoples, who prefer the active hunt and pursuit of game.

While the estimates of loss rate are very tentative, it is necessary to take them into consideration when assessing impacts of exploitation and status of stocks. In some cases they may be very high, making them in these cases the most important element of exploitation (see also narwhal section).

The sub-committee recommends that research on killed-but-lost and wounded-but-lost rates be initiated for each major type of white whale and narwhal hunt so that more confidence can be placed in statistics on removals. Such research might also examine sensible alternative technologies to reduce these losses particularly for those populations where significant removals now occur.

7.2.7 MSY and status of stocks

There are no estimates of MSY. The only estimate of sustainable yield is that of 5% by Sergeant for West Hudson Bay (SC/31/SM 6), but that estimate is based on the assumption that the population has been stable, an assumption that may well not be justified (discussed above). Sergeant reports that he plans to re-examine the data and refine the analysis. The sub-committee believes that at this point there is no secure basis for recommending any specific level of take as sustainable.

The sub-committee notes that the reported or estimated kills expressed as percentage of population size (Table 1) range from very low levels, e.g., less than 1%, to over 50% in the case of the Barents Sea complex (SC/31/SM 13). Some of the estimated exploitation rates exceed the probable level of gross reproductive rate (about 10%).

The sub-committee is especially concerned about the Cumberland Sound summer population, which is exploited at as much as 23% per year, has declined and is expected to continue to decline (SC/31/SM 5 and SC/31/SM 16).

The estimated rate for the Barents Sea complex is almost certainly incorrect, even given the relative shortness of the history of increased exploitation reported in the catch statistics (SC/31/SM 13). Catches of white whales in Soviet waters have declined steadily since 1960 (SC/31/SM 13) for two reasons:

(1) decline in hunting efficiency due to very large year to year variation in catches and
(2) a declining market for white-whale products (SC/31/SM 13). Even given a population decline, the extremely high rates of exploitation implied by the available statistics and population estimates must be incorrect; it is probable that the population estimates are incomplete. The sub-committee notes this situation with some concern and emphasizes the great importance of obtaining full and accurate relevant data (see Recommendations to Scientific Committee).

The West Greenland winter stock may also be exploited at or above probable MSY level. However, Kapel pointed out that the population of white whales occurring in West Greenland apparently has been able to sustain a catch of the magnitude 500–1,000 animals per year since around 1860. Great year-to-year fluctuations and variation in the regional distribution of catches have occurred during this long period. (Kapel and Peterson in IWC, 1979 and Winge 1902, Anon 1944a and b (SC/31/SM 22)).

7.3 Narwhal

7.3.1 Definition of stocks

The sub-committee reviewed the available information on distribution, migration, and stock identity. As stock structure is presently understood, narwhals are divided into three separate stocks. These are the Davis Strait – Baffin Bay stock, the East Greenland – Spitzbergen stock, and a tentatively identified stock in Foxe Basin, Canada. Kapel suggests that there may be a discrete sub-division of the Davis Strait – Baffin Bay stock that summers in the Thule and Melville Bay region. Braham reported on seven sightings of narwhal off Point Barrow, Alaska; five in spring and two in fall; the stock affinity of these is unknown. The Davis Strait – Baffin Bay group winters in the pack ice between Disco Bay and eastern Hudson Strait (SC/31/SM 16). Migration northward in spring is poorly described but is believed to be along the Greenland coast to the Thule and Melville Bay areas and through the central pack ice into Lancaster Sound and various summering areas in the Canadian archipelago. The tentatively identified Foxe Basin group is believed to winter in Hudson Strait, possibly overlapping with the Davis Strait – Baffin Bay stock. This population summers in the Foxe Basin region (Mansfield, et al., 1975).

The East Greenland – Spitzbergen stock extends through the whole extent of the East Greenland pack ice north to northwest Spitzbergen (Reeves, 1979). It has long been known to occur along the East Greenland coast.

7.3.2 Age determination and estimates of vital rates

An adequate technique of age determination does not exist at present, but Kemper reported that research on age determination is underway in Canada. Sergeant (SC/31/SM 6) has the opinion that the life history parameters of maturation rate and longevity may be similar to those of the white whale. The sub-committee believes that more research is needed to generate estimates of life history parameters for use in stock assessment. No estimates of vital rates were available to the sub-committee.

7.3.3. Estimates of net reproductive rates

No estimates have been made of net reproductive rates. Research on life history and reproductive rates is underway in Canada, including a field program of collection of life history samples (SC/31/ProgRep 3).

7.3.4. Estimates of population size

SC/31/SM 5 and 19 contain information on population size. Table 3 contains estimates from Davis (1978).

7.3.5 Catches

The available information on catches is presented in Table 3. The actual take in the Canadian Arctic may be greater than the reported take (SC/31/SM 9, SM 16 and SC/31/ProgRep 3).

7.3.6. Struck or killed-but-lost rates

Estimates of loss rates (Appendices 4 and 5) are comparable to those for white whales and are of equal concern to the sub-committee. In addition to the animals that are killed-but-lost, a higher proportion (42% of 48 animals) of the narwhals taken at the Pond Inlet ice edge had old bullet scars (SC/31/SM 9). Kemper reports that research to reduce hunting losses has begun in Canada.

Minority opinion on loss rate, by Sergeant

The estimate of average loss rate for the Canadian Arctic of 52% in Table 3, based on one year's data from one area may be too high, because 1978 was a severe ice year (SC/31/SM 19) and loss rates for ice-edge hunts are higher than for open-water hunts (Table 2, Hay and Sergeant, 1976).

Table 2

Loss rates from narwhal floe edge hunt and coastal (open water) summer hunt, Pond Inlet

Number lost	Total	Percent lost	Where	Observers
11	16	69	Floe edge	Finley *et al.* (Doc 9) 1979
5	21	25	Open water	Finley *et al.* (Doc 9) 1979
7	46	15	Open water	Hay & Sergeant, 1976

More observations are clearly needed, especially on the ice-edge hunt and on the relative numbers of narwhals caught in the different types of hunt in the course of three to five seasons. This should not preclude speedy action to reduce loss rates.

7.3.7 MSY and status of stocks

No estimates exist of sustainable yield, and status relative to initial size could not be estimated for any of the three stocks based on the data available to the sub-committee. The sub-committee urges that the involved governments be requested to initiate the studies necessary to obtain data for assessment and management of the stocks.

8. REVIEW OF SMALL CETACEANS OF THE SOUTH ATLANTIC COAST OF SOUTH AMERICA

The documents reviewed by the sub-committee were SC/31/SM 1, 2, 3, 4, 23 and Prog Rep Argentina.

8.1 Distribution

Mermoz (SC/31/ProgRep Argentina) and Goodall and Polkinghorn (SC/31/SM 2) presented sightings from land observers in Tierra del Fuego and shipboard in the area from the Rio de la Plata to the Falkland Islands (Islas Malvinas), South Georgia and the Antarctic Peninsula. Brownell and Praderi (SC/31/SM 23) presented a historical review and new sighting data for Commerson's dolphin, *Cephalorhynchus commersonii.* Beach surveys (Goodall and Cameron, SC/31/SM 1) were made for observation and collection of stranded cetaceans.

New sightings of *Lagenorhynchus cruciger, L. obscurus* and *Globicephala melaena* were made within the ranges suggested by Brownell (1974, *Antar. Map Folio Ser.* 18: 13 – 19) and former reports (*Rep. int. Whal. Commn* 27: 507–20; L29). The following new data were noted.

Lagenorhynchus australis. Five significant offshore sightings were made of this normally coastal species.

Cephalorhynchus commersonii. The known coastal distribution was amplified by many sightings. Offshore sightings were made in the Drake Passage, NE of Burdwood Bank and south and east of Cape Horn. One sighting at Isla Desolacion, at the western end of the Strait of Magellan, is the most westerly record for the species.

C. eutropia. Thirteen records of this rare species were made in the Fuegian and Patagonian channels, Chile.

Lissodelphis peronii. This species is notable due to its absence; only one tentative sighting was reported.

Orcinus orca. This was a frequently recorded species, particularly near the Antarctic Peninsula and in the Beagle Channel, Tierra del Fuego.

Phocoena spinipinnis. Four sightings in inshore areas were reported, three of them from Tierra del Fuego. These are the first sightings south of the Strait of Magellan.

8.2 Definition of stocks

Knowledge of the small cetaceans of the Atlantic coast of South America is insufficient to determine stocks at present.

8.3 Directed take

Goodall (SC/31/SM 3) summarized information on recent and some historical directed takes. There have been occasional incidents of directed kill because of real or supposed competition with fish or for sport.

About 23 *Lagenorhynchus australis* were harpooned for *centolla* (southern king crab) bait in Tierra del Fuego, Argentina, in July – August 1978, but this has since been stopped.

Dolphins are harvested for *centolla* trap bait in Magallanes, Chile. *C. commersonii* and *L. australis* are utilized, in numbers estimated at 2350, from July – January 1976–77 and possibly a similar number taken in 1978–79. This take is now prohibited by Chilean law but enforcement in the vast inland channels which these species and the fishermen frequent is difficult.

8.4 Incidental take in fisheries

Pontoporia blainvillei is taken in a beach seining fishery in Brazil (Castello, pers comm) and about 250 are taken per year in shark nets in Uruguay (Praderi, SC/31/SM 4). Specimens for study are collected in both cases.

Incidental takes in fisheries occur along the Argentine coast, but there is no information at present on numbers involved, although it seems fairly low.

Some *C. commersonii* are taken in nets for *centolla* and *robalo* in the Province of Santa Cruz, and by *robalo* nets in Tierra del Fuego (Goodall, SC/31/SM 3).

8.5 Population trends

The sub-committee expressed some concern about impact that recent exploitation may be having on small local populations of *C. commersonii* and *L. australis* in the Strait of Magellan region. Nothing is known about population trends along the Atlantic Coast of South America and more research is definitely needed.

8.6 Research programs

The present sighting program off the coast of southern South America and the Antarctic Peninsula will be continued and improved with assistance from the Argentine Navy and other agencies.

Research is under way at Rio Grande, Brazil; in Uruguay; in Buenos Aires and Peninsula Valdez, Argentina; and in Punta Arenas, Chile. All these programs are greatly hampered by lack of funds.

In Tierra del Fuego, Argentina, a field camp is planned at Bahia San Sebastian on the Atlantic coast due to the large number of strandings which occur there.

Training of local people to observe, collect and report cetacean observations and strandings will greatly improve local knowledge which is poor in all areas except Tierra del Fuego. There is a potential to expand these programs into Chile.

The OAS published a draft proposal of a 'Plan of Action for Marine Mammals', as a result of its meeting of experts in Puerto Madryn, Argentina, 12–16 September 1977. The priorities are research on endangered and poorly known species; specific research on *Phocoena spinipinnis, P. sinus* and *Pontoporia blainvillei;* sperm and Bryde's whales in the SE. Pacific; humpback whales in the E. tropical Pacific; and southern right whales. There is no information as to when this research will begin.

9. LIVE-CAPTURE FISHERIES

Argentina. Goodall (SC/31/SM 3) reported that in 1978 six Commerson's dolphins, *Cephalorhynchus commersonii,* were sent to Germany for display purposes, and four destined for Japan were confiscated by US authorities en route. Four more for Japan are authorized in 1979.

Mexico. Marcet Ocaña reported that during 1977, five to eight live bottlenose dolphins, *Tursiops,* were sent to the UK and in 1978, about 12 were sent to Switzerland and Germany for display and research. Dolphins are completely protected in Mexico.

South Africa. Two dusky dolphins, *Lagenorhynchus obscurus,* were caught in 1978 under permit for public display (SC/31/ProgRep 9). One died in transit, and the other died after 13 months in captivity.

Enactment of the MMPA in the US in 1977 led to live captures of several species in Mexico, but progress is being made in controlling these captures.

10. RECOMMENDATIONS TO THE SCIENTIFIC COMMITTEE

10.1 Concerning white whales and narwhals

(1) The sub-committee recommends that because the Cumberland Sound summering population of white whales has declined to an unknown but likely small fraction of its initial size, and because annual takes in recent years have amounted to as much as 23% (in 1977) of the population, a level almost certainly higher than even gross reproductive rate, the stock be classified as a Protection Stock and a catch limit of zero placed on it. The sub-committee further recommends that current research on the Cumberland Sound stock of white whales be continued and expanded. The research should include regular censuses of the summering population and estimates of gross recruitment. The inter-relationships of Cumberland Sound and Hudson Strait stocks should be examined. Full data on age, sex, size and reproductive status should be obtained from the catch, should there be one.

(2) The sub-committee is concerned about reports of very large catches of white whales in Canada along the Quebec coast of Hudson Strait and the northeast coast of Hudson Bay and the fact that no estimates of the size of the populations involved have ever been made. The sub-committee strongly recommends that Canada be requested to initiate research to determine the identity and size of the population(s) involved in this catch and to determine whether these populations are distinct from those in W. Hudson Bay.

(3) The sub-committee noted that the white whales that winter along the coast of West Greenland migrate to summering areas in the central Canadian High Arctic and in the Melville Bay-Thule areas of Greenland. Although catches in Greenland have been of the level of 400–1,500 animals annually for over 100 years and no population estimate is available for the latter summering groups, the sub-committee believes it highly probable that current levels of removals are higher than MSY for the overall population. The sub-committee recommends that these groups, which winter in west Greenland waters, be provisionally managed as one stock and that Canada and Denmark (Greenland) be urged to initiate a joint research program on this stock. Of particular importance is an accurate census of the numbers of white whales summering in Melville Bay – Thule District and Canadian and Greenland waters of Smith Sound and Kane Basin and analysis of inter-relationships among these and other summer populations. The program should also include more accurate determination of the killed-but-lost rates associated with the various types of hunts in Greenland and Canada.

(4) The sub-committee believes the catch levels for white whales that inhabit the Barents, White, Kara and Laptev Seas are substantially above even annual gross production or that the present population estimates are incomplete. The sub-committee, therefore, recommends that the USSR be requested to provide all available data to the next Scientific Committee Meeting. The analysis of these data should include a study of the components of the Barents Sea wintering group and an assessment of the stock or stocks involved.

(5) The main wintering grounds and composition of the Bering Sea group of white whales are largely unknown, and sizes and inter-relationships of the summering groups

are also poorly known, including those in Soviet waters. Although present removals from these groups may be sustainable, it is probable that harvests will increase as indigenous populations increase or alternative subsistence needs arise. For example, the white whale is one alternative to the bowhead. The sub-committee therefore recommends that national research programs be expanded and that a co-operative research program be instituted by the USA, USSR and Canada. These programs should begin soon and should include documentation of catch statistics, loss rates and characteristics of the hunt and collection of biological samples for determination of vital parameters. The temporal and spatial components of the populations should be determined, the populations censused and the inter-relationships among them identified.

(6) The sub-committee believes that management of the aboriginal/subsistence fisheries for white whales and narwhals should be considered by the Commission in the same manner as in the bowhead fishery in the Bering Sea and Arctic Ocean. White whales of some stocks and narwhals on the one hand and bowhead whales on the other both undergo long migrations, crossing national territorial boundaries. Both are taken by indigenous peoples using light craft and harpoons, with various modifications derived from modern technology. Whaling efforts for the two are interrelated, and scientific analysis of catch data should take this multispecies aspect of aboriginal whaling into consideration. Elements of modern cash economy have arisen in some regions and have modified value and use of carcasses of both bowheads and the smaller whales. The only substantive differences between the fisheries are in size of the whales and size of and organisation of the whaling crews involved, differences not justifying the radically different treatment presently given them. The sub-committee recommends that the Scientific Committee recommends to the Commission that the white whale (*Delphinapterus leucas*) and the narwhal (*Monodon monoceros*) be defined as 'whales' and listed in Paragraph 1 of the Schedule thus:

"white whale" (*Delphinapterus leucas*) means any whale known as white whale, beluga, belukha

"narwhal" (*Monodon monoceros*) means any whale known as narwhal, sea unicorn

so that the appropriate management procedures may be discussed and implemented in the future.

10.2. Other recommendations

(7) The sub-committee recommends that the research programme recommended for the northern bottlenose whale in 1977–78 be carried out and that the stock continue to be classified a Protection Stock with a zero catch.

(8) Noting that no stock assessment is possible with data in hand for the population of killer whales subject to small-type whaling in Norwegian waters, the sub-committee urges that Norway be requested to produce the necessary data on stock assessment at the 1980 meeting of the Scientific Committee. Pending availability of results of such assessment, the sub-committee recommends that Norway be requested to limit its catch in 1980 to not more than 52 whales, the average annual Norwegian coastal take over the 10 year period 1969–78.

(9) The sub-committee noted that the USSR is engaged in whaling for killer whales in the Antarctic. Because stock assessment has not been carried out for the stock(s) being fished, the sub-committee recommends that the USSR be requested to provide for the 1980 meeting of the Scientific Committee the data necessary for such an assessment, including any available data on sightings, sighting effort, sex, length, age, weight, reproductive condition and date and locality of capture of the killer whales taken since commencement of the Antarctic fishery for killer whales. The sub-committee further recommends that, pending the availability of the results of the stock assessment analyses, the USSR be urged to limit its take of Antarctic killer whales during the 1979–80 season to not more than 24 whales, the average annual take over the 10 year period 1969–78.

(10) The sub-committee notes the absence or incompleteness of statistics on the take in many fisheries, and recommends that more complete data be requested from member nations for:

(a) The Canadian white whale harvest, including statistics on fisheries in Quebec, Manitoba and Ontario.

(b) Takes of cetaceans incidental to net fisheries for tuna in the eastern tropical Pacific by Mexico, Panama, New Zealand and Peru as soon as possible.

(c) Takes of harbour porpoises in Passamaquoddy Bay by Canada and the USA and incidental takes in Eastern Canada.

(d) All catches, with reference to the completeness of the statistics, in particular to insure that the following minimum data are collected (as recommended in Scientific Committee Report, *Rep. int. Whal. Commn* 27: 31; and Resolution, Appendix 6, *Rep. int. Whal. Commn* 28: 30):

   (i) Species name, and local vernacular name where available
   (ii) Numbers caught
   (iii) Location of catch
   (iv) Biological data wherever it is possible to collect them
   (v) An appropriate indication of the intensity of catching effort and of the primary species caught, to which the sub-committee would add
   (vi) Day, month and year of capture.

These minimum data are also requested from nations that have recently joined the IWC.

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Appendix 1

AGENDA

1. Participants, agenda, and introductory remarks.
2. Review of documents submitted.
3. Review of management actions and research on northern bottlenose whale, striped dolphin, Dall's porpoise and harbour porpoise.
4. Other directed catches of small cetaceans.
5. Problems of interactions between fisheries and small cetaceans.
    - 5.1 Incidental takes.
    - 5.2 Direct conflicts and competition.
6. Effects of pollution and industrial development.
7. Review of definition and status of stocks of the white whale, *Delphinapterus leucas*, and the narwhal, *Monodon monoceros*.
    - 7.1 Increasing importance of the fisheries.
    - 7.2 White whale.
        - 7.21 Definition of stocks and trans-national boundary migrations.
        - 7.2.2 Age determination and estimates of vital rates.
        - 7.2.3 Estimates of net reproductive rates.
        - 7.2.4 Estimates of population sizes.
        - 7.2.5 Commercial and subsistence takes.
        - 7.2.6 Hunting loss rates.
        - 7.2.7 MSY and status of stocks.
    - 7.3 Narwhal.
        - 7.3.1 Definition of stocks.
        - 7.3.2 Age determination and estimates of vital rates.
        - 7.3.3 Estimates of net reproductive rates.
        - 7.3.4 Estimates of population sizes.
        - 7.3.5 Catches.
        - 7.3.6 Hunting loss rates.
        - 7.3.7 MSY and status of stocks.
8. Review of small cetaceans of the South Atlantic coast of South America.
    - 8.1 Distribution.
    - 8.2 Definition of stocks.
    - 8.3 Directed take.
    - 8.4 Incidental take in fisheries.
    - 8.5 Population trends.
    - 8.6 Research programs.
9. Live-capture fisheries.
10. Recommendations to the Scientific Committee.

Appendix 2

SUMMARY OF ACTIONS ON SMALL CETACEANS IN THE IWC, 1976–78

Year	Level	Mandate for management	Management n. bottlenose whale	Research on 4 spp. (n. bottlenose whale, striped dolphin, Dall's porpoise and harbour porpoise)
1976	Sub-comm.	Pointed out need for coverage of *all* takes, but recommend provisional coverage of directed take	Pointed out need for management action	Recommended
	Sci. Comm.	Referred to Commission	Proposed to discuss in 1977	Accepted
	Commission	Proposed to consider *all* takes in scientific forum and assumed provisional responsibility to manage directed takes (at least, to consider in Sci. Comm.)	Stated that should be considered for immediate action by Scientific Committee	Accepted
1977	Sub-comm.	Acknowledged responsibility to consider directed takes	Referred to full Scientific Committee	Not reported; again recommended
	Sci. Comm.	'Small-type whaling' redefined	Recommended zero catch limit	Strongly urged
	Commission	Accepted new definition of 'small-type whaling' and responsibility to manage, and *Resolved* to urge members to collect statistics on all small cetacean takes	Approved zero catch limit	Noted that Norway plans research
1978	Sub-comm.	Again pointed out need for international coverage of *all* cetacean takes in management	Recommended continued protection	Again recommended
	Sci. Comm.	Agreed	Agreed	Agreed
	Commission	Agreed; is urgent	Approved zero catch limit	Agreed

Appendix 3

LANDED CATCH OF WHITE WHALES IN NORTHERN QUEBEC AND LABRADOR IN 1975[1]

Area	Community	Catch
E. coast of Hudson Bay[2]	Great Whale River	26
	Inukjuaq	97
	Akudlivik	5
S. coast of Hudson strait	Sugluq	122
	Wakeham Bay	162
	Koartak	31
	Port Burwell, N.W.T.	8
Ungava Bay	Payne Bay	43
	Leaf Bay	7
	Fort Chimo	53
	George River	19
	Total	573[3]

1. From: Anonymous 1976. Research to establish present levels of harvesting by native peoples of northern Quebec. James Bay and Northern Quebec Native Harvesting Research Committee. Processed Rep. 230 pp.
2. Excludes community of Povungnituk which did not participate in the study.
3. Except for Port Burwell, the landed catch from these communities have not been reported to the IWC by Canada.

Appendix 4

AVERAGE REPORTED CATCH OF NARWHAL AND WHITE WHALE IN WEST GREENLAND

Including Estimates for Killed-but-lost Rates in Various Hunting Periods and Situations

	West Greenland South of Thule			Thule District		
Period	Average catch[1]	Estimated total removals[2]	Calculated loss rate %	Estimated catch[1]	Estimated loss rate[2] %	Estimated total removals
White Whale						
1967–70	1,023	1,265	19	~100	<10	50–200
1971–74	882	1,027	14	(50–200)		
Narwhal						
1967–70	285	376	24	~200	<5	100–300
1971–74	159	192	17	(100–300)		

[1] Catch data from Kapel, 1977; and Kapel and Petersen in IWC, 1979.

[2] Estimated total loss rates were calculated by apportioning the percent of the landed catch taken in various seasons (and therefore, hunting situations) as follows:

winter–spring hunts: 1 lost per 4 landed.
Savssats (winter): 1 lost per 2 landed.
open water (summer): 1 lost per 10 landed.
Thule summer hunt: (narwhal) — 1 lost per 20 landed.
(white whale) — 1 lost per 10 landed.

Catch statistics for NW., CW. and SW. considered separately; Thule hunt as above. Note that the *Savssats* may make up a large proportion of the catch in some years, thereby shifting the killed-but-lost percentage since *Savssats* are assumed to have 50 percent loss rate. *Savssats* occurred more frequently in the 1967–70 period than in 1971–74.

Appendix 5

ESTIMATED LOSS RATES (KILLED-BUT-LOST) IN WHITE WHALE HUNTS IN NORTH AMERICA

Location	Hunting method	Estimated loss ratio	References and notes
Cook Inlet, Alaska	Unknown	Low	Braham
Bristol Bay, Alaska	Unknown	Unknown	
Norton Sd St Lawrence Island Alaska	Boat, rifle and harpoon	<2/1 taken	Braham, via Eskimo whalers, Gambell I, Alaska
Kotzebue, Alaska	Boat, rifle and harpoon	..	Braham, via Eskimo whalers, Kotzebue, Alaska
NW coast of Alaska	Ice edge, rifle, boat	<5/1 taken	Braham, pers. obs., SC/31/SM 8
Mackenzie Delta, Canada	Boat, rifle, grapple, silty water	<1/2 taken	SC/31/SM 8
Eastern Canadian Arctic	Boat, rifle (some with harpoon), silty water (some cases)	..	Extrapolated from SC/31/SM 8

Appendix 6

CATCH STATISTICS SYSTEM AND RESEARCH PLAN ON SMALL CETACEANS IN JAPAN

1. Regular catch statistic system

'Annual report of catch statistics on the fisheries and agriculture' edited by the Department of Statistics, Ministry of Agriculture, Forestry and Fisheries provides 'number of small cetaceans caught' by area (prefecture), but all species are combined. Sizes of catch from 1971 through 1977 are included in Table 2 of the Japan Progress Report.

2. Collection of supplemental information on small cetaceans by Fishery Agency

This will appear at irregular intervals.

The statistics provide information for relevant years on 'number of small cetaceans caught' by (1) prefecture, (2) species and (3) type of fishing gear, with some information about the fisheries concerned. The first work started last year, and the materials are now being examined and compiled.

3. Research plans

(1) The Fisheries Agency plans to develop techniques to prevent damage to fisheries such as the Iki Island fishery (planned for 1978–80 at the Fisheries Technology Laboratory and at Takai University). The plan includes a research project for controlling the behaviour of dolphins by means of broadcast of audible high-frequency sound.

(2) Project is planned for observation of behaviour and collection of biological materials (1980–82, Far Seas Fisheries Lab.). For the project, two areas have been selected in which to concentrate the observation effort:

  (1) an area off the east coast of northern Honshu dominated by a cold current;
  (2) an area around Iki and Tsushima Islands dominated by a warm current.

Annex J

WHALE MARKING – PROGRESS REPORT 1979

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Information on the progress of whale marking is available in the following Progress Reports:– Australia, Canada, Iceland, Japan, New Zealand, Norway, South Africa, USA, USSR. Recent marking is also referred to in SC/31 Docs 10, 11, 24, 25 and 30; Doc 25 being a Report on the Southern Hemisphere Minke Whale Assessment Cruise 1978/79.

A total of 1,228 large whales was marked in the Southern Hemisphere during the Antarctic season 1978/79 and in 1978 and 1979. This total includes whales marked in the two IDCR Marking Cruises, and comprises 16 blue, 37 fin, 25 sei, 82 Bryde's, 9 humpback, 800 minke, 5 southern right and 254 sperm whales, all marked with Discovery-Type marks (Table 1).

In the North Atlantic 194 whales were marked in 1978 and 1979; 24 fin, 2 humpback, 162 minke and 6 sperm whales. One of the humpbacks and 14 of the minke whales were marked with Visual Streamer Marks.

In the North Pacific 203 whales were marked in 1978 and 1979; 4 blue, 11 fin, 27 sei, 52 Bryde's, 5 humpback, 6 minke, 29 gray and 69 sperm whales. Two of the fin whales and 3 of the humpback whales were marked with radio tags in Alaskan waters. The 29 gray whales were marked with colour coded visual tags.

One killer whale was marked by the USSR in the Antarctic in the 1978/79 season.

Recoveries of Discovery-Type marks so far reported for the 1978 season are from 4 minke whales in the North Atlantic, and from 1 Bryde's whale 1 sperm whale in the North Pacific. In the Southern Hemisphere marks are reported from 5 minke whales marked in the IDCR programme.

Proposed marking programmes

A number of marking programmes were recommended in the sub-committee reports presented to the Scientific Committee. These were reviewed, approved and given priorities by the committee. In Table 2 they are listed in order of priority with the estimated number of marks and marking guns required for each programme, and their estimated costs.

At 1 June there were in stock, or on order, the following quantities of marks:

	In stock	On order
12 Bore Standard	150	1200
12 Bore Increased Charge	225	200
.410 Standard	1300	—

Outstanding payments for marks previously received and those on order can be covered by funds available from the 1978/79 IWC, IDCR and SMRU contributions to whale marking, but no funds are available for the shipment of any of the marks at present in stock or on order. Any additional orders to provide marks and marking guns for programmes which cannot be met from the marks already available, will have to be paid for by the IWC contribution to whale marking for 1979/80 (it was £4,000 in 1978/79) and by additional contributions, reserved for whale marking, made to the Research Fund.

8070

ROLE OF A NEMATODE IN NATURAL MORTALITY OF SPOTTED DOLPHINS

Parasitism was advanced by Delyamure (1955) as a major factor in the natural mortality of cetaceans, and infestation by helminths was implicated strongly as the cause of death in some stranded common dolphins (*Delphinus delphis*) (Ridgway and Dailey 1972). Severe and irreversible lesions of the skull of dolphins (*Stenella* spp.) caused by a nematode (*Crassicauda* sp.) were more prevalent among young animals than among old animals (Dailey and Perrin 1973). The reduced frequency of lesions with age indicated that severely infected animals were dying of the parasitic infection or a related cause (Dailey and Perrin 1973). We report quantification of mortality related to *Crassicauda* sp. in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific.

METHODS AND MATERIALS

The skulls of 704 spotted dolphins were examined for lesions (Table 1). This represented a stratified random sample of dolphins of this species killed incidentally in the purse-seine fishery for tuna in the eastern tropical Pacific Ocean (Perrin 1968). Dailey and Perrin (1973) examined 126 specimens and classified them to age by using growth layers in dentin as an index. The infection rate that they reported was used to develop a stratified random sampling procedure for our study. The number of dolphins with 3 or fewer dentinal layers needed to achieve a coefficient of variation of 0.25 for the estimate of infection rate was calculated. Similarly, the number with >3 layers needed for a coefficient of variation of 0.50 was calculated. The 126 dolphins previously aged were apportioned into these strata. Additional dolphins were selected at sea, on the basis of body length, to achieve the sample size of 704.

The heads were cleaned and examined, and morphometric and sutural data used in age estimation were recorded. The extent of nematode-related damage on the underside of the skull was classified as none, some, or severe (≥ 2 extensive lesions).

Three methods were used to deter-

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mine relative age of the dolphins. First, for the original sample of 126, the actual number of layers was determined from examination of teeth. Second, for the remaining dolphins less than 150 cm long, the number of layers was estimated on the basis of length, using the model of Perrin et al. (1976). Finally, for the remaining dolphins >150 cm long, a regression model was fitted, in which layers were estimated from total length and data on sutural closure for the skulls. The model was

$$Y = e^{b_0} \prod_{i=1}^{8} X_i^{b_i}$$

where Y = number of dentinal layers, and the variables (X) are based on morphometrics and sutural features of the skull. The model was fitted using a multiple linear regression after a logarithmic transformation.

Mortality and infection rates were calculated using the exponential model $N_t = N_0 \exp[(r - m)t]$, or $N_t = N_0 \exp(a + zt)$, where N_t = % of skulls with lesions at dentinal layer t, N_0 = % with lesions at initial age $t = 0$, m = exponential rate of parasite-related mortality, r = exponential rate of parasite infection, $z = r - m$ = net exponential rate of change in lesion frequency, and $a = \ln(N_0)$. Estimates of the parameters z and N_0, along with standard errors, were calculated using weighted regression formulas after a ln transformation (Steel and Torrie 1960:2181). Standard errors for the parameters were calculated as in Steel and Torrie (1960).

Because we have no data other than frequency of lesions, we cannot partition z into its components of infection and mortality. However, if we assume that past some age at which there is a peak frequency of lesions no significant new lesions occur, then after that age the net change z is equal to the mortality rate m. The same assumption may be made for young animals, such that $z = r$, if no significant mortality occurs during this time. However, the latter assumption possibly is unjustified. Another assumption basic to these analyses is that infection does not affect the likelihood of capture of the dolphins; i.e., an infected dolphin is not more likely to be killed incidentally in the tuna fishery than is an uninfected one.

Table 1. Lesion rate in spotted dolphin skulls, males and females combined.

Age (layers)	Skulls examined (N)	Skulls with lesions	
		N	%
1	68	2	3
2	31	4	13
3	41	6	15
4	21	1	5
5	15	4	27
6	18	4	22
7	18	2	11
8	37	2	5
9	60	5	8
10	63	5	8
11	79	5	6
12	88	10	11
13	82	1	1
14	38	2	5
15	20	1	5
16–19	25	1	4

RESULTS

The parameters of net change in skull lesions for animals with 8 or more dentinal layers were $\hat{z} = -0.1308$, $SE_{\hat{z}} = 0.2940$, $\hat{a} = -2.4563$, and $SE_{\hat{a}} = 0.2081$. When $\hat{z} = -0.1308$, there is a reduction in frequency of lesions of 12.3% per layer (range of 1 SE truncated at zero is 0–34.6%). The maximum frequency of occurrence of lesions is 8.6% of the population (7.0–10.6%) at 8 layers.

Assuming there is no new infection in adults, the mortality rate of infected animals from parasite-related causes is

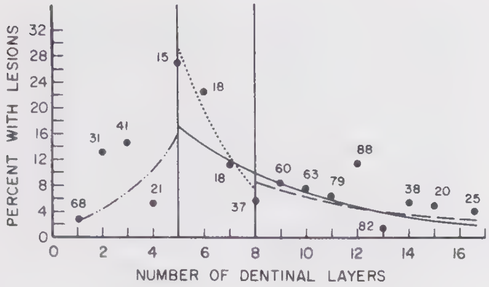

Fig. 1. Relative frequency of spotted dolphin skulls with nematode lesions vs. age in dentinal layers. Numbers are the numbers of skulls examined. Curves were fitted separately for ages (layers) 1–5, 5–8, 5–19, and 8–19.

12.3% per layer. Given that only 8.6% of the population at 8 layers is infected, the mortality rate for the population is 1.1% (0.0858 × 12.3%) with an SE range of 0–3.7%.

The decrease in animals with lesions was 36.0% per layer for dolphins with 5–7 layers. This implies that the lesion-related mortality rate for all animals of this age was 10.6% (0–43.9%). This does not differ from the rate for the older animals (8 or more layers), because of a large standard error resulting from a total frequency of only 10 lesions in the 5- to 7-layer category. Only 51 animals with 5–7 layers were in the sample, and the 7 of these directly aged had no lesions. Therefore, the standard error of the mortality rate was large. However, it is not unreasonable to assume that the mortality rate decreases with age. A more precise estimate may be made by grouping age strata. Grouping all animals with 5 or more dentinal layers, the rate of decrease in spotted dolphins with lesions was 15.5%. The mortality rate for all animals with 5 or more dentinal layers was 2.6% (0–6.2%).

The net infection rate, as exemplified by the presence of lesions, was calculated in a similar fashion using frequencies from animals with 5 or fewer layers. The rate of increase in lesions is estimated to be 53.9% per layer. The fitted rates with the grouped data are presented in Fig. 1.

DISCUSSION

The net infection rate by the nematode that results in lesions in young animals approximates 50% per layer. Then there is a period of reduction in parasite-correlated mortality of approximately 10% per layer for layers 5 through 7. After 8 layers are achieved, the rate of lesion-related mortality drops to approximately 1%.

Whatever the proximate cause of mortality (brain damage, increased susceptibility to predation, etc.), the ultimate cause may be the nematode parasite itself. Future studies of *Crassicauda* sp. in spotted dolphins should include a search for brain histopathology associated with bone lesions. Also required are the specific identity of the parasite and elucidation of its life history. Although related spirurid nematodes use intermediate hosts, potential transplacental transmission or transmission via milk to the nursing calf should be investigated. A closely related form (or even possibly the same form), may cause reproductive failure in Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (Geraci et al. 1978) through invasion of mammary glands.

Estimates of natural mortality of the spotted dolphin in the eastern tropical Pacific range from 7 to 9% per year (Southwest Fish. Cent. Adm. Rep. LJ-76-29, 1976). Estimates of total mortality in 1975 were 10–13% per year. If dentinal layer deposition occurs at 1 layer per year, the rounded-off estimates of nematode-induced annual mortality are 1% per year for animals with 8 or more dentinal layers, and 3% per year for those with more than 5 layers. Higher rates of layer deposition (e.g., 2 per year) would mean even higher rates of parasite-related annual mortality. These estimates represent 11–14% of the natural mortality of the population, and support the concept that parasitism constitutes a major factor in natural mortality of small cetaceans.

Acknowledgments.—The dolphin specimens were collected by several field technicians aboard commercial tuna seiners. Especially helpful were J. M. Coe, D. B. Holts, and C. W. Oliver. J. G. Mead, C. W. Potter, and others at the National Museum of Natural History carried out the labor of preparing >500 skulls. J. Zweifel helped with the original experimental design. M. D. Dailey, J. G. Mead, S. H. Ridgway, and J. R. Geraci read the manuscript and offered suggestions for its improvement.

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POPULATION ESTIMATES AND YIELD-PER-RECRUIT ANALYSIS FOR THE SPINY LOBSTER, *PANULIRUS MARGINATUS*, AT NECKER ISLAND

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ABSTRACT

Data from commercial fishermen and research sampling for lobster fishing at Necker Island are examined. The abundance of lobster appears to be very heterogeneous with the greatest abundance in the northwestern part of the Necker bank. Estimates of virgin population size and catchability for this region are 125,000 legal lobsters and 3.94×10^{-5} per trap-night, respectively. The estimated range of sustainable yield from the northwest region based on the minimum legal size of 8.25-cm carapace length and the present population size is 10,000 to 21,000 legal lobsters per year. Yield-per-recruit analysis indicates that substantially greater yields may be possible if the minimum legal size is reduced from 8.25 cm. However, this latter result is based on strong assumptions about recruitment which can only be confirmed by field tests.

Necker Island
spiny lobsters
sustainable yield
yield per recruit

INTRODUCTION

Commercial spiny lobster, *Panulirus marginatus*, fishing began on a regular basis off Necker Island in the Northwestern Hawaiian Islands in November 1976. Seven commercial fishing vessels from Honolulu reported lobster catches during the period from November 1976 through April 1979. Some of these vessels trapped in the area frequently while others trapped only occasionally.

This report analyzes and summarizes commercial and research data for the *P. marginatus* fishery off Necker Island during the period from November 1976 through April 1979. Estimates of virgin population size, catchability, and sustainable yield are obtained and a yield-per-recruit analysis is performed. The commercial data consists of monthly totals of the number of legal lobsters caught and the effort expended (Table 1).

TABLE 1. TOTAL MONTHLY CATCH (IN NUMBERS) AND EFFORT (IN TRAP-NIGHTS) IN THE COMMERCIAL FISHERY FOR LEGAL LOBSTERS AT NECKER ISLAND, OCTOBER 1976-APRIL 1979

Date	Region I		Region II		Total	
	Catch	Effort	Catch	Effort	Catch	Effort
1976						
Oct.	107	73	--	--	107	73
Nov.	616	156	--	--	616	156
Dec.	984	276	--	--	984	276
1977						
Jan.	10,030	1,656	1,599	1,081	11,629	2,737
Feb.	--	--	--	--	--	--
Mar.	--	--	--	--	--	--
Apr.	--	--	--	--	--	--
May	15,588	3,480	67	53	15,655	3,533
June	7,132	1,936	461	122	7,593	2,058
July	9,727	2,447	24	75	9,751	2,522
Aug.	5,404	1,832	678	534	6,082	2,366
Sept.	10,524	2,944	293	120	10,817	3,064
Oct.	2,901	916	58	120	2,959	1,036
Nov.	1,885	600	--	--	1,885	600
Dec.	2,485	824	--	--	2,485	824
1978						
Jan.	1,314	254	203	92	1,517	372
Feb.	978	300	--	--	978	300
Mar.	3,687	1,482	54	60	3,741	1,600
Apr.	3,022	719	398	112	3,420	831
May	3,160	687	--	--	3,160	687[1]
June	2,940	1,260	--	--	3,849	1,724
July	2,167	603	--	--	2,167	603
Aug.	2,014	585	--	--	2,014	585
Sept.	202	246	--	--	202	246
Oct.	1,574	606	1,373	401	2,947	1,007
Nov.	116	56	5,222	2,349	5,338	2,405
Dec.	--	--	7,040	3,139	7,040	3,139
1979						
Mar.	1,563	658	--	--	1,563	658
Apr.	1,925	958	--	--	1,925	958

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[1] Two stations with no positions.

A legal lobster is defined as a lobster with a carapace length equal to or exceeding 8.25 cm. These data were collected by National Marine Fisheries Service (NMFS) observers aboard commercial vessels or were reported in catch reports submitted by the vessels' owners. The unit of effort is measured as one baited trap fished on the lobster ground for one night, henceforth referred to as a trap-night. The research data consist of total number and effort, as well as length and sex, for lobsters caught at sampling sites from the RV Townsend Cromwell.

Necker Island is surrounded by a large bank (Figure 1). The commercial catch by position indicates that the fishermen have primarily trapped in the northwest region of this bank, indicated as Region I in Figure 1. There were 90,368 legal lobsters trapped in Region I from January 1977 through April 1979; only 17,740 legal lobsters were trapped on the rest of the bank (Region II) during the same period (Table 2). The catch per unit effort (CPUE) in Region II (Figure 2) shows considerable variation, and some of the more recent values for CPUE approach those for Region I (Figure 3). However, because of the lack of a longer series of catch and effort data for Region II, this report will focus only on Region I. By isolating Region I for study, we are making the assumption that the lobster population in this region is closed. This may not be an unreasonable assumption for adult lobsters because tagging experiments by NMFS indicate minimal migration. However, in the case of larval recruitment this may not be the case and for the long term, the assumption of a closed population in Region I may not be valid.

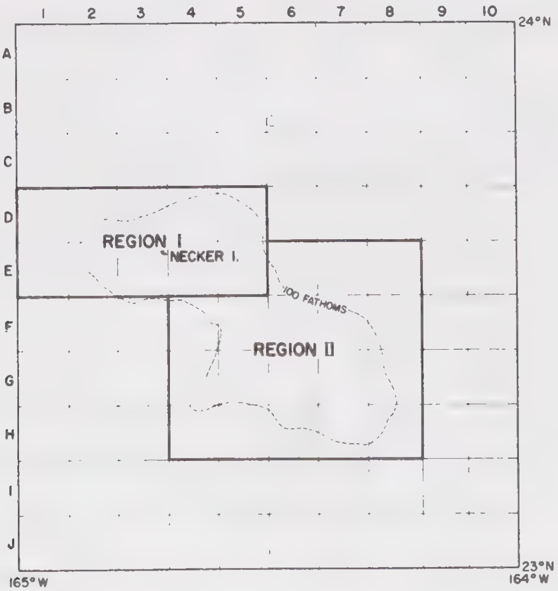

Figure 1. Necker bank

TABLE 2. THE ANNUAL CATCH (IN NUMBERS OF LOBSTERS), EFFORT EXPENDED (IN TRAP-NIGHTS), AND CATCH PER UNIT EFFORT FOR LEGAL LOBSTERS AT NECKER ISLAND BY COMMERCIAL VESSELS FROM JANUARY 1977-APRIL 1979

Year	Catch	Effort	Catch Per Unit Effort
Region I			
1977	65,676	16,635	3.95
1978	21,201	6,798	3.12
1979 (1/1-4/30)	3,491	1,616	2.16
Region II			
1977	3,180	2,105	1.51
1978	14,290	6,153	2.32
Combined (Regions I and II)			
1977	68,856	18,740	3.67
1978	35,491	12,951	2.74

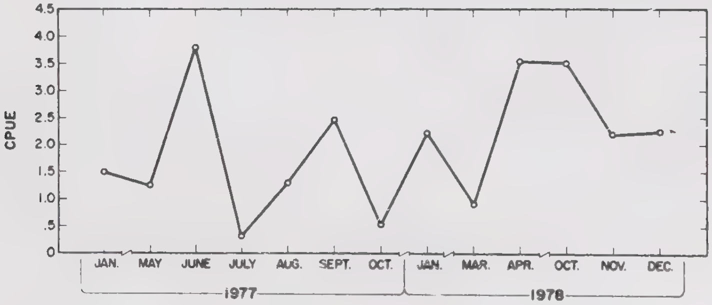

Figure 2. Catch per unit effort (in legal lobsters per trap-night) from Region II at Necker Island

RELATIVE ABUNDANCE

Catch per unit of effort provides a measure of relative abundance. Changes in CPUE over time can result from changes in population structure and size, as well as changes in fishery methods and gear. In the case of the lobster fishery at Necker between November 1976 and April 1979, the changes in fishing methods and gear have been minimal. A graph of CPUE for legal lobsters from Region I on a monthly basis is presented in Figure 3. Considerable month-to-month variation as well as a declining trend is apparent.

One reason for some of the month-to-month variation in CPUE is that the monthly CPUE is computed by pooling the catch and effort for all the

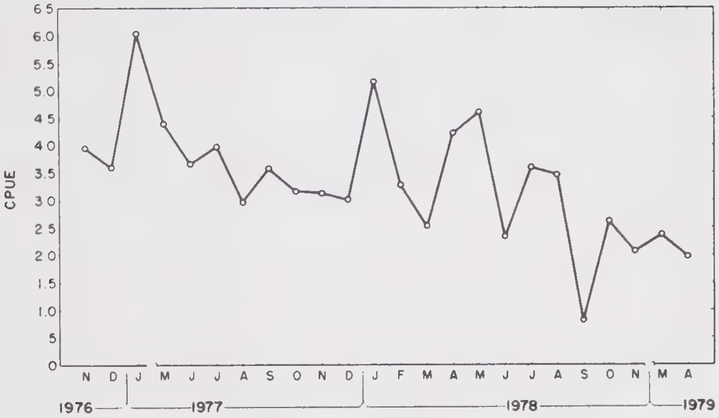

Figure 3. Catch per unit effort (in legal lobsters per trap-night) from Region I at Necker Island

vessels reporting trips to Necker during the month. These vessels are not always the same vessels but a subset of the seven commercial vessels which comprise the fleet.

Catch per unit effort computed on an annual basis has declined each year from 1977 to 1979, although the 1979 figure should be treated with caution because it is based on only an effort of 1,616 trap-nights and may change when more 1979 data are available (Table 2).

A regression of CPUE against month, weighted by effort, indicates that at the 5% level the decreasing trend in CPUE for 1977 is significant while the trend in 1978 is not. The CPUE for January 1977 and January 1978 represents a sharp increase from the preceding and following months indicating a possible seasonal trend which should be examined as more data become available.

The percentage of legal lobsters in the total lobster catch provides an index of the proportion of legal lobsters in the population to the total lobster population. A decrease in this index could mean that the number of legal lobsters in the population has been reduced and/or the number of sublegal lobsters in the population has increased due to increased reproduction, survival, or immigration. We found that the percentage of legal lobsters in the catch for the RV Townsend Cromwell decreased from 54.2% in November 1976 to 23% in May 1979 (Table 3).

POPULATION ESTIMATES

The primary approach we selected to estimate population size was a method proposed by Allen (1966) (see Appendix 1). Basically, this method consists of a least squares procedure which estimates population size and catchability by minimizing the sum of squares between the actual catch and the predicted catch based on effort.

TABLE 3. THE AMOUNT OF EFFORT EXPENDED (IN TRAP-NIGHTS) AND PERCENTAGE OF LEGAL LOBSTERS CAUGHT AT NECKER ISLAND BY THE RV *TOWNSEND CROMWELL*

Date	Effort (Trap-Night)	% Legals in Catch
	Region I	
Oct.-Nov. 1976	145	54.2
May 1977	32	40.0
Oct. 1977	116	42.0
Mar. 1978	57	35.0
Oct.-Nov. 1978	104	37.1
May 1979	48	22.8
	Region II	
Sept.-Oct. 1977	234	62.6
Mar. 1978	61	81.0
Oct. 1978	52	67.0

We used the monthly commercial catch and effort data from November 1976 through April 1979 to estimate population size and catchability. Allen's model assumes natural mortality and recruitment operate in the population. In its most general form, this model assumes that the rate of natural mortality is constant while recruitment may vary over time. This most general form requires that the use supplies estimates of the natural mortality rate and the recruitment rates. We do not have any size and age data which might allow us to estimate these parameters and consequently, we used a simplified version of Allen's model. We assumed that the ratio of the rate of natural mortality to the recruitment rate ($e^{-M}/1-W_i$) in Appendix 1 is constant. Given effort, we then estimated this constant as the value which gave the best fit of predicted catch to actual catch. We feel the assumption that the ratio (rate of natural mortality to recruitment rate into the fishery) is constant may not be unreasonable for the 2-year period of our study. If it takes 6 or more years for a lobster to grow from larval stage to legal size, and if the majority of the mortality occurs during the early years of life, then even an intense reduction of the population of legal lobsters in 1977 will not have a major effect on the ratio of natural mortality rate to recruitment rate until 6 years later.

The plots of actual monthly catch and predicted monthly catch estimated by Allen's method are presented in Figure 4. The fit of the model to the data is good. Based on this method, we estimate that there were 132,406 legal lobsters in Region I at the beginning of November 1976. This number declined to 68,571 legal lobsters by April 1979. A plot of the monthly estimated population size is given in Figure 5. As could be expected from the catch and CPUE data, the population size of legal lobsters dropped severely during 1977 and decreased very slowly during 1978.

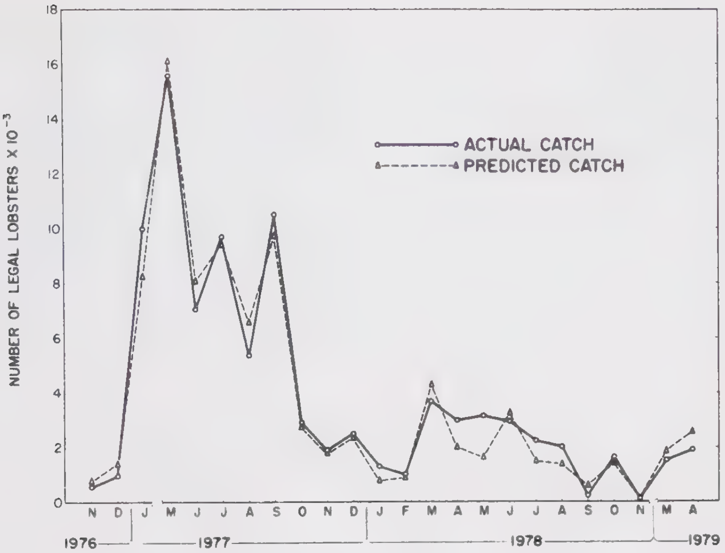

Figure 4. Catch predicted from Allen's model versus actual catch of legal lobsters from Region I at Necker Island

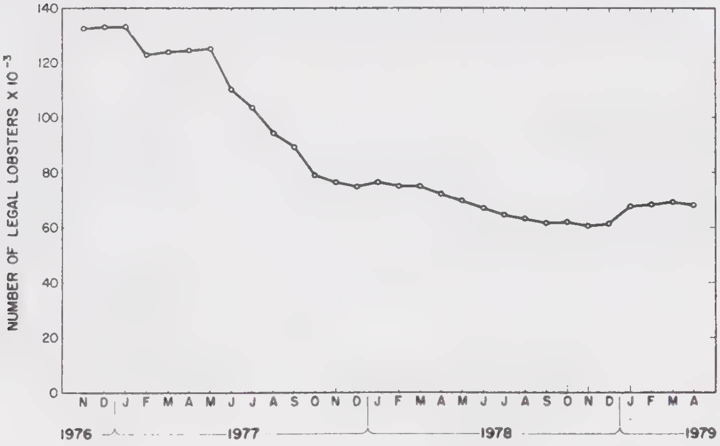

Figure 5. Estimated population size of legal lobsters from Allen's model for Region I at Necker Island

As an independent check on the results obtained by Allen's method, we used Leslie's method of population estimation. This method is used to estimate population size and catchability in situations where there has been intensive fishing of a closed population over a short period of time. Since this method applies to fishing over a short period of time, we assume that natural mortality and recruitment are negligible.

We noticed from Table 1 that trapping was very intense from May through August 1977. We used these data to estimate the population size of legal lobsters at the beginning of May 1977 and the catchability by Leslie's method. The estimated population size and catchability obtained from Leslie's method is in agreement with the estimates obtained by Allen's method (Table 4).

TABLE 4. A COMPARISON OF THE ESTIMATES FROM THE LESLIE AND ALLEN METHODS

	Leslie	Allen
N_{May}	127,000	125,000
q	3.58×10^{-5}	3.94×10^{-5}

N_{May} is an estimate of the number of legal lobsters in Region I beginning May 1977; q is the catchability coefficient.

Lobster yield-per-recruit analysis

We can explore the relationship between size at entry into the fishery (minimum carapace size) and yield with the Beverton-Holt equilibrium yield equation. We will assume that over the range of minimum legal sizes of interest, the number of recruits to a given size is constant, that the lobster growth can be approximated by a von Bertalanffy equation, and that the lobster weight can be expressed as: weight = a $(\text{length})^b$. We then write the yield per recruit into the fishery Y/R as:

$$\frac{Y}{R} = \left(\frac{F}{K}\right)\left(W_\infty\right)\left(e^{Zt_m}\right)\left[B\left(X,\ b,\ \frac{Z}{K}\right)\right]$$

where F is the fishing mortality, K is the growth coefficient for the von Bertalanffy curve, W_∞ is the asymptotic lobster weight, $Z = F + M$, M is the natural mortality, $t_m = t_{min} - t_o$, where t_{min} is the minimum age of entry into the fishery and t_o is the age of zero length in the von Bertalanffy curve, and $B(X, b, Z/K)$ is the incomplete beta function evaluated at $X = e^{-Kt_m}$, and b is the allometric coefficient.

We will evaluate Y/R at several levels of fishing effort and several minimum carapace lengths. We selected fishing effort (f) at the following levels (trap-nights): 2,500, 5,000, 7,500, 10,000, 12,500, and 15,000. Based on these values of f we can estimate F as F = qf where q = 4 × 10^{-5} from Allen's method. We selected the following values for the minimum legal carapace length: 6.75, 7.25, 7.75, and 8.25 cm. The value of t_m corresponding to these lengths can be estimated from the von Bertalanffy curve. We determined W_∞ to be 3,580 g and the coefficient b in the weight-length relationship as b = 2.6 from data in McGinnis (1972). There is not any one data set for lobster growth which appears sufficiently reliable. Results from tagging and modal analysis by NMFS gives the estimates: K = 0.26/yr and L_∞ = 12.5 cm. Observations by McDonald of an 18-cm carapace curve suggests L_∞ could be as high as 18 cm. We, thus, performed the yield-per-recruit analysis for the following sets of K and L_∞ values: (K = 0.05, L_∞ = 18 cm), (K = 0.1, L_∞ = 15 cm), (K = 0.2, L_∞ = 12 cm). We used the relationship:

$$\frac{F + M}{K} = \frac{(L_\infty - \bar{l})}{\bar{l} - l_{min}}$$

where l_{min} is the minimum carapace length, $\bar{l}$ is the mean carapace length of the population above l_{min}, and F and M are the fishing and natural mortality, respectively (Beverton and Holt, 1956).

We are able to estimate the ratio M/K by taking a length-frequency distribution from a sample of the population taken from Necker Island in November 1976--before any substantial fishing effort was applied to the region. This sample, consisting of 744 lobsters, estimated M/K at approximately 3.5 for L_∞ = 12 cm. For the yield-per-recruit analysis, we used values for M/K as 2, 3, and 4.

From the results of the yield-per-recruit analysis, we determined the carapace length from among the set 6.75, 7.25, 7.75, and 8.25 cm, which gave the greatest yield (Table 5). In most situations, a minimum carapace length of 6.75 cm achieved the maximum yield per recruit. Only when M and M/K are low and L_∞ is large is the yield per recruit achieved with a minimum carapace length greater than 6.75 cm.

TABLE 5. CARAPACE LENGTH (IN CENTIMETERS) AT WHICH THE MAXIMUM YIELD PER RECRUIT (IN GRAMS) IS OBTAINED

		Fishing Effort					
		2,500	5,000	7,500	10,000	12,500	15,000
$\frac{M}{K} = 2$	K = 0.05, L_∞ = 18	7.75	8.25	8.25	8.25	8.25	8.25
	K = 0.1, L_∞ = 15	6.75	6.75	6.75	7.25	7.25	7.75
	K = 0.2, L_∞ = 12	6.75	6.75	6.75	6.75	6.75	6.75
$\frac{M}{K} = 3$	K = 0.05, L_∞ = 18	6.75	6.75	7.25	7.25	7.75	7.75
	K = 0.1, L_∞ = 15	6.75	6.75	6.75	6.75	6.75	6.75
	K = 0.2, L_∞ = 12	6.75	6.75	6.75	6.75	6.75	6.75
$\frac{M}{K} = 4$	K = 0.05, L_∞ = 18	6.75	6.75	6.75	6.75	6.75	6.75
	K = 0.1, L_∞ = 15	6.75	6.75	6.75	6.75	6.75	6.75
	K = 0.2, L_∞ = 12	6.75	6.75	6.75	6.75	6.75	6.75

An examination of the yield-per-recruit results suggest that an adoption of a 6.75-cm minimum carapace length could, in the worst case ($K = 0.05$, $L_\infty = 18$, $M = 0.1$, and $F = 15{,}000$), result in a 15% decrease in yield per recruit from the minimum carapace length of 8.25 cm, and at best ($K = 0.2$, $L_\infty = 12$, $M = 0.8$, $F = 1{,}500$), achieve a 167% increase in yield-per-recruit over an 8.25-cm minimum carapace length (Table 6). Clearly, these results should be interpreted cautiously because we have no evidence to suggest that the level of recruitment will remain unchanged when the minimum carapace length is lowered to 6.75 cm. However, the magnitude of the possible increase in yield which may be achieved with a reduction from the existing minimum carapace length should serve as impetus for further study and testing.

TABLE 6. YIELD-PER-RECRUIT (IN GRAMS) AS A FUNCTION OF FISHING EFFORT (IN TRAP-NIGHTS) AND MINIMUM LEGAL CARAPACE LENGTH (IN CENTIMETERS) FOR SELECTED GROWTH AND MORTALITY PARAMETERS

	Fishing Effort					
l_{min}	2,500	5,000	7,500	10,000	12,500	15,000
	$\frac{M}{K} = 4$, $K = 0.2$, $L_\infty = 12$					
6.75	124	216	287	343	388	425
7.25	90	157	210	252	286	314
7.75	64	112	150	180	205	226
8.25	44	78	105	126	144	159
	$\frac{M}{K} = 3$, $K = 0.1$, $L_\infty = 15$					
6.75	210	305	355	384	402	415
7.25	194	285	334	364	383	397
7.75	177	262	310	340	360	373
8.25	160	239	284	313	332	346
	$\frac{M}{K} = 2$, $K = 0.05$, $L_\infty = 18$					
6.75	318	339	335	327	321	315
7.25	321	351	351	347	342	338
7.75	321	358	363	361	349	356
8.25	319	362	371	372	371	370

CONCLUSIONS

The analysis of commercial catch and effort data indicating the decline in CPUE from 3.95 in 1977 to 3.12 in 1978 strongly suggests that a population size of 65,676 legal lobsters is not sustainable with a CPUE of 3.90. This is further supported by the decline in the percentage of legal lobsters per trap from the Cromwell sampling data. The fact that we do not reject the hypothesis that CPUE did not decline during 1978, based on the test of the slope of the regression line, suggests that a yield of 21,201 legal lobsters per year may be sustainable with a CPUE of about 3.00. We can use the result of Allen's model to compute the surplus production which can be harvested without reducing the population size. This value is obtained by multiplying the population size of legal lobsters by the ratio of the natural mortality rate to the recruitment rate for legal lobsters and subtracting the initial population size. We estimated the population size at the beginning of 1979 to be 67,766 legal lobsters and the ratio of the monthly rate of natural mortality to recruitment to be 1.0116. Consequently, for 1979, we estimate that slightly over 10,000 legal lobsters can be harvested for the year without reducing the population size of legals. Thus, based on the data presented here, the annual surplus production of legal lobsters in 1979 is estimated to be between 10,000 and 21,000.

Finally, due to the results of our theoretical yield-per-recruit analysis, it is suggested that future research undertake field trials to ascertain the impact of a lower legal size on yield per recruit.

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APPENDIX 1

Allen's population estimation procedure

A method developed by Allen (1966) was used to estimate population size at time t (N_t), catchability (q) given effort at time t (X_t), and catch (C_t). M is the natural mortality, W_i is the proportion of the new recruits in the exploited stock for the ith season, and A is the ratio of the number of animals that die per month to the number of animals that are recruited per month. The essential relationships of this model are given below:

Year 1 Initial population $= N_1$

Survival to beginning of next season $= (N_1 - C_1)e^{-M}$

Expected catch $= \left(N_1 - \frac{C_1}{2}\right)qX_1$

Year 2 Initial population $= N_2 = \frac{(N_1 - C_1)e^{-M}}{1 - W_2}$

Survival to beginning of next season $= \left[\frac{(N_1 - C_1)e^{-M}}{1 - W_2} - C_2\right]e^{-M}$

Expected catch $= \left[\frac{(N_1 - C_1)e^{-M}}{1 - W_2} - \frac{C_2}{2}\right]qX_2$

Continuing in this way we can show that at the beginning of year t the population equals

$$N_t = \frac{e^{-(t-1)M}}{\prod_{i=2}^{t}(1-W_i)}\left[N_1 - C_1 - \frac{C_2(1-W_2)}{e^{-M}} \cdots \frac{C_i \prod_{j=2}^{i}(1-W_j)}{e^{-(i-1)M}} \cdots \frac{C_{t-1}\prod_{j=2}^{t-1}(1-W_j)}{e^{-(t-2)M}}\right]$$

$$= A_t\left[N_t - f(C)_{t-1}\right],$$

where

$$A = \frac{e^{-(t-1)M}}{\prod_{i=2}^{t}(1-W_i)}$$

and

$$f(C)_{t-1} = C_1 + \sum_{i=2}^{t-1}\frac{C_i}{A_i}\ .$$

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PRELIMINARY RESULTS FROM ECOSYSTEM MODELING AT FRENCH FRIGATE SHOALS

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ABSTRACT

The marine ecosystem at French Frigate Shoals is discussed and preliminary results of the modeling work are presented. Application of the Bulk Biomass Model produces biomass estimates and turnover rates for species groups at French Frigate Shoals which consist of seabirds, monk seals, tiger sharks, small sharks, turtles, small pelagics, carangids, reef fishes, lobsters, snappers and groupers, shrimps, nearshore scombrids, and benthos.

French Frigate Shoals
ecosystem modeling
Bulk Biomass Model

INTRODUCTION

The objective of our ecosystem modeling is to draw on the expertise and results of the people and projects of the Northwestern Hawaiian Islands (NWHI) program to develop a quantitative and dynamic model of the marine ecosystem around French Frigate Shoals (FFS) in the NWHI. Because the model is dynamic, it may prove to be useful as a management tool and may also help to identify components of the ecosystem where additional research attention is needed.

Our approach to modeling begins with the top carnivores and works down to the primary producers. We have identified 13 species groups which form the components of our ecosystem. Rather than initially try to model the entire NWHI, we have restricted our modeling work to the ecosystem at FFS.

METHODS

The mathematical Bulk Biomass Model, which is described in detail by Laevastu and Favorite (1978), served as the tool for our ecosystem modeling. This model produces estimates of the biomass of the species groups in the ecosystem which is at equilibrium, based on growth, mortality, and consumption values specified by the user. The ecosystem is said to be at equilibrium conditions when the biomass of a species group is unchanged from one year to the next, although seasonal changes within a year are permitted. This is achieved when biomass growth equals its removal due to predation, natural mortality, and fishing mortality.

The population size of species which are the apex predators, typically birds and mammals, are considered fixed and are not changed during iterations of the model. The biomass of all other species groups are varied during the iterations until equilibrium conditions are met. The biomass values for species groups estimated at equilibrium conditions are heavily dependent on accurate estimates of the quantitative composition of the diet for each species group (Livingston, 1978). This report will deal only with the application of this tool to the ecosystem at FFS.

The ecosystem

We have defined 13 species groups which represent the components of the reef and nearshore ecosystem. These groups which will subsequently be described in detail are: seabirds, monk seals, tiger sharks, small sharks, turtles, small pelagics, carangids, reef fishes, lobsters, benthos, snappers and groupers, nearshore scombrids, and shrimps.

French Frigate Shoals

French Frigate Shoals is located at 166°10'W, 24°50'N, approximately midway along the chain of islands and banks comprising the NWHI. It is described by Bakus (in Bryne, 1979) as a "crescent-shaped reef on a circular submerged platform about 18 miles in diameter (almost an atoll). The shoals form a large lagoon, bordered on one side by 12 sand islets (total area 56 acres) with a small rock pinnacle (La Perouse Pinnacle, ∿ 1 acre) near the center of the platform. The highest elevation is generally 5 feet above sea level except for La Perouse Pinnacle (135 feet high)." The area is an important nesting ground for the green turtle, *Chelonia mydas*, various species of seabirds, and the Hawaiian monk seal, *Monachus schauinslandi*.

The ecosystem of interest to our modeling is the reef and nearshore community. We have defined the reef habitat as the area from 0 to 55 m (0 to 30 fathoms) (Gosline and Brock, 1976). The nearshore community is defined as the area ranging from 55 to 365 m (30 to 200 fathoms). These definitions applied to FFS yield a reef habitat of 761.6 km^2 and a nearshore habitat of 407.7 km^2. The sum of these regions consists of a circular area centered at FFS with a radius of approximately 20 km (Table 1).

Seabirds

Studies from the U.S. Fish and Wildlife Service (FWS) indicate that the following seabirds are found in abundance at FFS: sooty tern, *Sterna fuscata*; black noddy, *Anous tenuirostris*; brown noddy, *A. stolidus*; great frigatebird, *Fregata minor*; red-footed booby, *Sula sula*; wedge-tailed

TABLE 1. AREA BY DEPTH AT FRENCH FRIGATE SHOALS

Reef Habitat		Nearshore Habitat	
Depth (fathoms)	Area (km^2)	Depth (fathoms)	Area (km^2)
0-10	461.5	30-40	34.9
10-20	264.9	40-50	37.3
20-30	35.2	50-100	95.7
Total	761.6	100-200	239.8
		Total	407.7

shearwater, *Puffinus pacificus*; Laysan albatross, *Diomedea immutabilis*; and black-footed albatross, *D. niaripes*. The total seabird population is estimated by FWS to be 320,000 birds (C. Harrison, U.S. Fish and Wildlife Service, Honolulu, Hawaii 96850, personal communication, October 1979). Detailed studies of stomach contents of birds in the NWHI have been undertaken jointly by the National Marine Fisheries Service (NMFS) Honolulu Laboratory and FWS. Based on this information, we estimate the diet of the birds to be 65% small pelagics including flyingfish, opelu, and squid, 10% juvenile tunas; 10% juvenile carangids; 10% juvenile snappers; and 5% zooplankton.

Monk seals

A census of the Hawaiian monk seal indicates a population of about 200 adults and pups in 1978 (Fiscus et al., 1978). Stomach contents of dead seals, regurgitated samples, and feces have been studied to determine their diet (National Marine Fisheries Service). Based on this work, we estimate that their diet is 85% reef fishes including eels and octopus, 5% lobsters, and 10% benthos. The extent of predation on seals by sharks is uncertain. While numerous seals are seen with scars which could have been caused by shark attacks, observations at Laysan provide little direct evidence of such attacks even though sharks are abundant in the shallow waters (B.W. Johnson and P.A. Johnson, National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, Washington 98115, personal communication, October 1979).

Tiger sharks

The tiger shark, *Galeocerdo cuvier*, is the predominant apex predator at FFS. Analysis of stomach contents from tiger sharks caught in the NWHI suggest that their diet consists of 45% reef fishes, 20% seabirds, 24% smaller sharks, 4% small pelagics, 4% lobsters, 2% turtles, and 1% monk seals (M. DeCrosta, Hawaii Cooperative Fishery Research Unit, University of Hawaii, Honolulu, Hawaii 96822, personal communication, December 1979).

A measure of the relative abundance of tiger sharks in the NWHI was obtained by Taylor and Naftel (1978). Eighteen sets of shark longlines at Pearl and Hermes Reef and FFS with a total of 388 hooks produced a catch rate of 10.31 tiger sharks/100 hooks. A report on shark fishing around Oahu suggests that a catch rate of six tiger sharks/100 hooks represented a density of 1.21 tiger sharks/km of 10-fathom contour (Lawrie, 1977). Extrapolating this density estimate for the NWHI catch rate, we obtain a figure of 2.08 tiger sharks/km or a total of 415 tiger sharks at FFS. We feel that most of these sharks would feed in the reef habitat where food is more abundant.

Small sharks

This is a group of nearshore warmwater sharks other than the tiger shark. Based on observations and catches at FFS, this group includes the grey reef shark, *Carcharhinus amblyrhynchos*, the galapagos shark, *Carcharhinus galapagensis*, the small blacktip shark, *C. limbatus*, the sandbar shark, *C. milberti*, the dusky shark, *C. obscurus*, and the whitetip reef shark, *Triaenodon obesus*. They occur in great numbers in the deeper waters outside of the reef, but also work their way into the shallow waters of the inner reef. These sharks prey primarily on the smaller reef fishes, but their diet also includes pelagic fish, bottom-dwelling fish, stingrays, crustaceans, squid, and octopus. Based on analysis of stomach contents (M. DeCrosta, personal communication, December 1979), we estimate their diet as: 75% reef fishes, 5% lobsters, 10% small pelagics, 5% carangids, and 5% snappers and groupers in the reef habitat; and 58% small pelagics, 20% carangids, 15% snappers and groupers, 5% small sharks, and 2% reef fishes in the nearshore habitat.

Relative abundance for this group of sharks has been estimated in the NWHI at 9.8 sharks/100 hooks, based on longline catches (Taylor and Naftel, 1978). Around Oahu, a catch rate of 2.3 sharks/100 hooks was estimated to correspond to a density of 0.7 sharks/km along the 10-fathom contour (Lawrie, 1977). Extrapolating this density based on the catch rate for NWHI, we estimate a density of 2.9 sharks/km along the 10-fathom contour or 597 sharks at FFS. Visual observations of researchers who have worked at FFS suggest that this number is too low. We have arbitrarily chosen density figures of 10 sharks/km^2 for the reef habitat and 5 sharks/km^2 for the nearshore habitat. Based on a mean weight of 30 kg, we obtain biomass estimates of 300 kg/km^2 for the reef habitat and 150 kg/km^2 for the nearshore habitat.

Turtles

This group consists of the green turtle. Census counts indicate a population of 50 to 100 resident adult and 100 to 200 resident juvenile turtles at FFS (Balazs, 1979). However, during the breeding season, the population increases from 200 to 500 adults. Their diet consists principally of the following types of algae: *Codium arabicum*, *Caulerpa racemosa*, *Turbinaria ornata*, *Spyridia filamentosa*, *Rosenvingea orientalis*, and *Lobophora variegata* (Balazs, 1979). Their main predator is the tiger shark.

Small pelagics (small pelagic fishes and mollusks)

This group consists of small surface pelagic fishes and squid including flyingfish, exocoetids, opelu, *Decapterus* spp., akule, *Trachurops* crumenophthalmus, needlefish, belonids, and halfbeaks, hemiramphids. We estimate the diet of this group to be 80% zooplankton, 7% phytoplankton, and 13% small pelagics. Information which would enable direct biomass estimation is very limited. We have reliable figures on the seabird population of FFS and the bird diet. Based on this information, the minimum biomass of small pelagics necessary to meet bird predation would be 3,000 kg/km^2 in the nearshore habitat and 300 kg/km^2 for the reef habitat.

Carangids (carangids and large carnivores)

This is a group of active, fast-swimming carnivores which includes the white ulua, Caranx ignobilis; omilu, C. melampygus; ulua, Carangoides ferdau; kahala, Seriola dumerili; uku, Aprion virescens; and barracuda, Sphyraena barracuda. These carangids are found both in the reef and nearshore regions. Based on an analysis of stomach contents (M. DeCrosta, personal communication, December 1979), we estimate the diet of this group to be 15% zooplankton, 60% reef fishes, 15% lobsters, and 10% carangids in the reef region; and 15% zooplankton, 60% small pelagics, 5% reef fishes, 10% snappers, and 10% carangids in the nearshore region.

Researchers have remarked on the apparent low abundance of carangids at FFS relative to other banks in the NWHI. The biomass estimate of 400 kg/km^2 for both reef and nearshore habitat used for this area is based on very limited fishing data and transect dives (H. Okamoto, Hawaii Division of Fish and Game, Honolulu, Hawaii 96813, personal communication, December 1979; and E. Hobson, Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, California 94920, personal communication, December 1979).

Reef fishes (reef fishes and octopuses)

This group consists primarily of the coral reef fishes, excluding the snappers, groupers, and carangids. Their habitat ranges from the surge zone down to depths of 55 m (30 fathoms).

Studies of the reef habitat and transects are currently ongoing at FFS (H. Okamoto and E. Hobson, personal communications, December 1979; R.W. Grigg, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii 96744; and J. Parrish, U.S. Fish and Wildlife Service, Honolulu, Hawaii 96850, personal communications, October 1979). These observations suggest that 12% of the area from 0 to 18 m (0 to 10 fathoms) is rich in reef fishes, 17% is moderate, and 71% is sparse. We will assume that the area in depths from 18 to 55 m (10 to 30 fathoms) is entirely a sparse habitat. A total of 36 transects produced estimates of fish biomass as follows: for a rich habitat 163,666 kg/km^2 (1,460 lb/acre); for a moderate habitat 16,815 kg/km^2 (150 lb/acre); and for a sparse habitat 1,569.4 kg/km^2 (14 lb/acre). This gives an average density of reef fishes at FFS of 15,000 kg/km^2 (134 lb/acre).

The density estimates of 163,666 kg/km^2 (1,460 lb/acre) for a rich habitat is in agreement with two estimates of standing crop determined from a rotenone study in Kaneohe Bay of 123,310 kg/km^2 (1,100 lb/acre) and 92,819 kg/km^2 (828 lb/acre) (Brock et al., 1979). Further, Goldman and

Talbot (1975) concluded from a survey of the literature that a maximum standing crop in a coral reef is about 201,780 kg/km^2 (1,800 lb/acre).

Estimates of the composition of reef fishes by weight from the Great Barrier Reef indicate that 10% are planktivores, 36% benthic feeders, and 54% carnivores (Goldman and Talbot, 1975).

Lobsters (lobsters and crabs)

This group includes the spiny lobsters, Panulirus marginatus and P. penicillatus, the slipper lobster, Scyllarides squammosus, and various crabs. The abundance of lobsters appears to be relatively low at FFS. Trapping data and transect studies indicate that the lobster population here is very low compared to other regions in the NWHI (R. Uchida, Southwest Fisheries Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, personal communication, October 1979). Based on this information, we selected a density of 200 kg/km^2 in the reef region and 50 kg/km^2 in the nearshore habitat. Lobsters are bottom feeders which prey primarily on benthos.

Benthos

The benthic community is typically rich, diverse, and well-developed. Organisms in this community include the sponges, algae, benthic fish, gastropods, bivalves, holothuroids, annelids, asteroides, ophiuroids, echinoids, crustaceans, and anthozoans. Members of the benthos may be carnivores, herbivores, or detritivores. An ongoing project is studying this community at FFS (R. Grigg and J. Parrish, personal communication, October 1979).

Snappers and groupers

This is a commercially important group of food fishes including opakapaka, Pristipomoides filamentosus; kalikali, P. sieboldii; gindai, P. zonatus; onaga, Etelis carbunculus; ehu, E. marshi; uku, Aprion virescens; hapu'upu'u, Epinephelus quernus; and butaguchi, Caranx cheilio. Fishermen report that these bottomfishes are caught predominantly between 75 and 220 m (40 and 120 fathoms). They are all active, carnivorous fish which prey on small fish, shrimp and other crustaceans, and macrozooplankton. Based on analysis of stomach contents, we estimate their diet to be 15% zooplankton, 60% benthos, 5% snappers, and 20% shrimps (R. Humphreys, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, personal communication, December 1979).

Based on our analysis of an intensive bottomfishing experiment in Guam (Ikehara et al., 1972), we arrived at an estimate of bottomfish biomass as 4.3 x 10^3 kg/nmi of the 100-fathom contour. We estimate the length of the 100-fathom contour at FFS to be 85 nmi and assume that 90% of the snapper and grouper biomass are in the nearshore region. We obtain estimates of snapper and grouper density in the reef region as 48 kg/km^2 and in the nearshore region as 808 kg/km^2.

Shrimps

This group, consisting primarily of Heterocarpus ensifer and Penaeus spp. is found in abundance between 225 and 375 m (125 and 200 fathoms). Estimates of density from trapping and trawling in the main islands are 50 kg/km^2 over this habitat range (Struhsaker and Yoshida, 1975). They are detritivores.

Nearshore scombrids (nearshore scombrids and carnivores)

This is a group of commercially important tunas and tunalike fish, and includes skipjack tuna, Katsuwonus pelamis; kawakawa, Euthynnus affinus; yellowfin tuna, Thunnus albacares; and ono, Acanthocybium solandri. Mahimahi, Coryphaena hippurus, and the rainbow runner, Elagatis bipinnulatus, also belong in this group. The members of this group are all pelagic or nearshore pelagic species which largely occupy the surface waters. The kawakawa is an inshore pelagic fish and has been observed foraging over the reefs in shallow water at FFS. These fishes are all active, fast-swimming carnivores and are opportunistic feeders. Their diets have been observed to consist predominantly of small fish, juvenile fish (tunas, snappers, carangids), squid, stomatopods, and megalops (Yoshida, 1979). Based on stomach content analysis, we estimate the diet of this group to be 20% zooplankton and 80% small pelagics.

The input data required by the Bulk Biomass Model are summarized for all species groups in Tables 2, 3, and 4.

TABLE 2. GROWTH AND FOOD CONSUMPTION RATES IN PERCENTAGE OF BODY WEIGHT PER MONTH

Species Group	Growth Rate	Food Consumption Rate
Tiger sharks	--	48
Monk seals	--	240
Seabirds	--	450
Small sharks	6	48
Turtles	3	180
Small pelagics	8	30
Carangids	4	60
Reef fishes	10	30
Lobsters	6	23
Benthos	6	24
Snappers and groupers	3	30
Shrimps	5	30
Nearshore scombrids	6	30

Note: Natural mortality due to factors except predation is 0.2%; fishing mortality = 0.

TABLE 3. INITIAL DENSITY ESTIMATES USED AS INPUT

Apex Species	Reef Habitat (Number)	Nearshore Habitat (Number)
Seabirds	40,000	280,000
Monk seals	150	50
Tiger sharks	250	150
Prey Species	**Reef Habitat (Biomass (kg/km^2))**	**Nearshore Habitat (Biomass (kg/km^2))**
Small sharks	300	150
Turtles	7	7
Small pelagics	300	3,000
Carangids	400	400
Reef fishes	15,000	500
Lobsters	200	50
Benthos	15,000	3,000
Snappers and groupers	50	800
Shrimps	5	50
Nearshore scombrids	50	350

TABLE 4. FOOD COMPOSITION (PERCENTAGE OF DIET BY SPECIES GROUPS)

Reef Habitat	Nearshore Habitat
Small sharks:	Small sharks:
75% Reef fishes	58% Small pelagics
10% Small pelagics	20% Carangids
5% Lobsters	15% Snappers and groupers
5% Carangids	5% Small sharks
5% Snappers and groupers	2% Reef fishes
Turtles:	Turtles:
100% Benthos	100% Benthos
Small pelagics:	Small pelagics:
80% Zooplankton	80% Zooplankton
13% Small pelagics	13% Small pelagics
7% Phytoplankton	7% Phytoplankton
Carangids:	Carangids:
60% Reef fishes	60% Small pelagics
15% Lobsters	10% Snappers and groupers
15% Zooplankton	10% Carangids
10% Carangids	5% Reef fishes
	15% Zooplankton

TABLE 4. FOOD COMPOSITION (PERCENTAGE OF DIET BY SPECIES GROUPS) (Continued)

Reef Habitat	Nearshore Habitat
Reef fishes:	Reef fishes:
54% Reef fishes	54% Reef fishes
36% Benthos	36% Benthos
10% Zooplankton	10% Zooplankton
Lobsters:	Lobsters:
100% Benthos	100% Benthos
Benthos:	Benthos:
50% Zooplankton	50% Zooplankton
30% Phytoplankton	30% Phytoplankton
20% Benthos	20% Benthos
Snappers and groupers:	Snappers and groupers:
60% Benthos	60% Benthos
20% Shrimps	20% Shrimps
15% Zooplankton	15% Zooplankton
5% Snappers and groupers	5% Snappers and groupers
Shrimps:	Shrimps:
100% Benthos	100% Benthos
Nearshore scombrids:	Nearshore scombrids:
70% Small pelagics	70% Small pelagics
25% Zooplankton	25% Zooplankton
5% Nearshore scombrids	5% Nearshore scombrids
Seabirds:	Seabirds
65% Small pelagics	65% Small pelagics
10% Nearshore scombrids	10% Nearshore scombrids
10% Carangids	10% Carangids
10% Snappers and groupers	10% Snappers and groupers
5% Zooplankton	5% Zooplankton
Seals:	Seals:
85% Reef fishes	85% Reef fishes
10% Benthos	10% Benthos
5% Lobsters	5% Lobsters
Tiger sharks:	Tiger sharks:
54% Reef fishes	54% Reef fishes
30% Small sharks	30% Small sharks
7% Lobsters	7% Lobsters
7% Small pelagics	7% Small pelagics
2% Turtles	2% Turtles

RESULTS AND DISCUSSION

The estimates of biomass, consumption, and turnover presented in Table 5 are based on computer runs simulating 80 years of ecosystem time with the input data from Tables 2, 3, and 4. There are still slight time trends in the biomass values for several of the species groups so these results do not yet represent an equilibrium solution; however, they are probably sufficiently close to an equilibrium solution to be useful for the purposes of discussing the model and input values. We have used relatively low food consumption rates for all species groups so the resulting biomass values represent the minimum sustainable biomass (Laevastu and Favorite, 1978).

TABLE 5. AVERAGE BIOMASS (IN WET WEIGHT, KG/KM^2) (B), ANNUAL CONSUMPTION (PRODUCTION) (IN WET WEIGHT, KG/KM^2) (C), AND TURNOVER (T = C/B) FOR REEF AND NEARSHORE REGIONS

Species	Reef Region			Nearshore Region		
	B	C	T	B	C	T
Small sharks	63.7	54.0	0.85	18.7	16.2	0.87
Turtles	9.3	3.6	0.39	3.5	0.7	0.20
Small pelagics	537.9	593.6	1.10	4,942.7	5,878.6	1.19
Carangids	157.0	135.1	0.86	937.4	1,022.0	1.09
Reef fishes	14,395.5	17,370.7	1.21	521.0	760.3	1.46
Lobsters	178.1	141.4	0.79	44.3	42.0	0.95
Benthos	9,580.9	13,981.6	1.46	1,235.3	1,970.3	1.60
Snappers and groupers	133.3	88.7	0.67	1,058.8	1,173.6	1.11
Shrimps	22.4	24.0	1.07	30.3	18.5	0.61
Nearshore scombrids	59.9	54.0	0.90	425.8	378.0	0.89
Total	25,138.0	32,446.7	1.29	9,217.8	11,260.2	1.22
Zooplankton	--	32,130.0	--	--	22,571.0	--

For most of the species groups, the estimated biomass values in Table 5 are not far from the initial estimates. This is particularly reassuring for reef fishes where we feel we have a reliable initial estimate. One exception is the estimated shark biomass, which appears low. This is due to heavy and perhaps, an unrealistic estimate of predation on smaller sharks by tiger sharks.

Data compiled after our computer work, which quantifies the distribution and relative abundance of benthos at FFS, coupled with standard production computation suggest that the production of benthos in the reef habitat should be about three times the value we obtained (R. Grigg, personal communication, February 1980). This information will be used to change our input estimates for future computer work. In the nearshore habitat, our estimated production agrees with his calculations.

Our estimated annual production for the reef region, excluding the benthic, zooplankton, and phytoplankton production, is 18,465.1 kg/km^2. This agrees with an estimated production of 22,000 kg/km^2/yr for a similar community on a reef in Bermuda (Bardach, 1959).

We have not attempted to model the phytoplankton and zooplankton production for the ecosystem. The computer program does, however, determine the total ecosystem zooplankton requirement based on the inputed diet composition values for all the species groups. The annual zooplankton consumption for the reef region is 32,130 kg/km^2 and for the nearshore region is 22,571 kg/km^2. Based on a transfer coefficient of 10%, this zooplankton production requires a phytoplankton production of 321,300 kg/km^2 and 225,710 kg/km^2 in the reef and nearshore regions, respectively. Primary production for the nearshore region has been estimated as 365,000 kg/km^2 (J. Hirota, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii 96744, personal communication, December 1979).

The predation on the species groups by seabirds, seals, and tiger sharks is approximately twice as high in the nearshore region as in the reef region (Table 6). This is due to the predation of birds on small pelagics in the nearshore region.

TABLE 6. ANNUAL CONSUMPTION BY APEX PREDATORS (SEABIRDS, MONK SEALS, AND TIGER SHARKS) IN KG/KM^2

Species	Reef Region	Nearshore Region
Small sharks	43	9
Turtles	3	1
Small pelagics	288	1,967
Carangids	48	273
Reef fishes	871	145
Lobsters	53	7
Benthos	83	10
Snappers and groupers	43	303
Shrimps	0	0
Nearshore scombrids	43	302
Total	1,475	3,017

FUTURE RESEARCH

There are two directions for future research. First, research directed toward improving estimates of biomass, growth rates, food composition, and food conversion is needed to improve the accuracy of the input to the model. Some of this research is already planned as part of the specific projects in the NWHI investigation. However, in some cases, specific projects are being proposed at NMFS to obtain the necessary data. One example of this is an intensive bottomfishing experiment we are planning at a small and isolated bank to estimate the standing stock of snappers and groupers per nautical mile of a given depth contour.

The second aspect of future research consists of model sensitivity analysis, simulation, and modification. We will vary input parameters to reflect our degree of certainty about the input values and observe the changes in equilibrium biomass values. We will simulate various fishing strategies to observe their impact on the ecosystem. Finally, we will consider modifications of some of the mathematical relationships in the model to incorporate our best understanding of the biological processes at French Frigate Shoals.

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Preliminary Population Estimate for the California Gray Whale based upon Monterey Shore Censuses, 1967/68 to 1978/79

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ABSTRACT

Annual shore censuses of southward migrating gray whales have been conducted for the past 12 years from points near Monterey, California by the National Marine Mammal Laboratory. To utilize these counts in an estimation of total population size, a series of experiments were conducted during the 1978/79 migration. Specific goals were to (1) determine what proportion of whales pass by out of sight offshore, and (2) identify and measure sources of observer bias in estimating the number of individuals in each group and its distance from shore. For 1, aircraft transects were flown perpendicular to the coast near the census stations, and distances of whales from shore were recorded. For 2, groups of experienced and naive observers made independent estimates of numbers within and distances to group of passing whales. A true count of number in each group was made from a circling aircraft, and a true measure of distance was made with an inclinometer. A preliminary application of the experimental results to the census data indicates a population size of at least 16,500 ± 2,900 gray whales.

INTRODUCTION

Gray whales (*Eschrichtius robustus*) now only occur in the North Pacific Ocean and adjacent waters of the Arctic Ocean. The species also existed in the North Atlantic until a few centuries ago (Fraser, 1970; Rice and Wolman, 1971; Mitchell and Mead, 1977). There are presently two geographically isolated stocks: an eastern Pacific stock, which migrates between Baja California and the Bering and Chukchi Seas, and a western Pacific stock, which migrates between South Korea and the Okhotsk Sea. These are designated as the California stock and the Korean stock, respectively. The efforts described in this paper were carried out in an attempt to evaluate the population status of the California stock.

The California stock spends the summer mostly in the Chukchi and northern Bering seas, although a small proportion remains scattered along the west coast as far south as Baja California, Mexico (Darling, 1977; Hatler and Darling, 1974; S. Swartz, pers comm.). This stock leaves the feeding grounds in October and migrates down the North American coast to winter along the west coast of Mexico (Rice and Wolman, 1971; Rugh and Braham, 1979).

Henderson (1972) concluded, after analyses of historical data, that the population of California gray whales did not exceed 15,000 prior to initiation of commercial exploitation in 1846, notwithstanding Scammon's (1874) estimate of 'probably not over 30,000' from 1853 to 1856. In 1885/96 Townsend (1887) estimated that only 160 gray whales migrated south past San Simeon, California. Howell and Huey (1930) doubted 'whether more than a few dozen individuals survived', but K. W. Kenyon (pers. comm.) stated that he commonly observed gray whales migrating past La Jolla, California during the 1930s, and calculations by Ohsumi (1976) suggest that the stock attained its lowest size of 4,400 in 1875.

Systematic shore counts of the southward migration were initiated at Point Loma in San Diego, California (32°40'N; 130 m above sea level), in 1952/53 and continued intermittently until 1977/78 (Gilmore, 1960; Rice, 1961; Wolman and Rice, 1979). These counts indicated a steadily increasing population until 1959/60 (Table 1), but by the mid-1960s offshore observations revealed that, due to the trend of the coastline, the

Table 1

Counts of southward–migrating gray whales, 1952/53 to 1978/79[a]

	Number of whales counted	
Season	Point Loma[b]	Yankee Point and Granite Canyon[c]
1952/53	982	
1954/55	1,646	
1956/57	1,839	
1959/60	2,344	
1967/68	1,324	3,120
1968/69	1,154	3,081
1969/70		3,064
1970/71		3,034
1971/72		2,588
1972/73		3,304
1973/74		3,492
1974/75		3,348
1975/76	2,822	3,797
1976/77	3,648	4,058
1977/78	5,122	3,127
1978/79		3,568

[a] Data for 1952/53 to 1956/57 from Gilmore (1960).
[b] Total counts.
[c] 'Comparison period' only – 18 December to 4 February, except for 25 December and 1 January. Count made at Yankee Point until 1973/74, and at Granite Canyon thereafter.

majority of whales passed too far offshore to be seen from land (Rice, 1965). Increasing boat traffic also appeared to be causing an increasing proportion to migrate far offshore.

Starting in 1967/68, a shore count has been made every winter, at Yankee Point (36°29′N; 23 m above sea level from 1967/68 to 1974/75), or at Granite Canyon (3.7 km south of Yankee Point, 21 m above sea level) from 1975/76 to 1978/79. Previous observations had shown that few whales pass out of sight of land at these sites, and boat traffic is at a minimum. As the data from this location form a continuous series, and are less complicated by geography and boat traffic than are the Point Loma data, the present analysis is concentrated on the Monterey data.

METHODS

Each year the whale watch was made from 0700 to 1700 each day by two observers who alternated five-hour shifts. Observers watched seven days a week. The exact duration of the census has changed slightly from year to year, but it usually began on or before 10 December, and ended on or after 6 February (59 days). The coastal topography is relatively uniform between the census locations and Point Lobos to the north, and Point Sur to the south, and we believe that any differences in counts between Yankee Point and Granite Canyon due to geography would be negligible.

In the actual census procedure, the observer watched to the north for southward migrating whales coming into view. When a whale or group of whales was first sighted, the time was recorded, and a first estimate of the number of animals present was noted, but not recorded. The whales were then kept under observation until they were directly offshore from the station, usually about one-half hour later. At that time a final estimate of the number of individuals present was made and recorded, along with the time, and an estimate of the distance of the animals' path from shore at that point. Binoculars (7×50) were used as a visual aid. Distance estimates were generally made to within one of seven intervals: 0–¼ miles; ¼–½; ½–¾; ¾–1; 1–1½; 1½–2; 2+. Wind direction, Beaufort wind force, and notes on visibility conditions (fog, glare, etc.) were recorded continuously throughout the day.

Occasionally, only one of the two times was recorded. Often when an observer came on duty at 0700 h, there were whales passing directly offshore or to the south of the station, and consequently no north time was recorded. Also, when an observer ended the afternoon watch at 1700 h, there were often whales sighted to the north which had not yet passed directly in front of the station. In order to account for these missing data, an average elapsed time between the two time records was calculated for each observer, and missing times generated from this average difference. The time when the animals were directly offshore was used to categorize sightings for time of day analysis. Only sightings with this time recorded between 0700 and 1700 were used for abundance estimation.

As the data were transcribed for computer analysis during 1978, a relative visibility code (1 = 'excellent' to 6 = 'unacceptable') was assigned to each observation in an attempt to quantify the effects of visibility on the census results. Beginning in 1978/79, a quantitative visibility code was assigned to each sighting by the observers.

The yearly gray whale censuses (along with the bowhead census) are unique in that they are attempts at a complete count of that proportion of the population which passes during daylight hours. Consequently, while extrapolations to account for whales missed are small relative to other whale population estimates that are based on censuses of vast water areas, they are still an important aspect of the estimation procedure.

In order to extrapolate from recorded counts to an estimate of total population size, it is necessary to determine:

(1) Is there a consistent observer bias in estimating the number of individual whales present in a group? If so, what is that bias?
(2) What proportion of the population, if any, passes beyond sight of the observers?
(3) Are there diel variations in migration rate? Can we use the daylight counts to estimate the number passing at night?
(4) How much effect does weather (= visibility) variation have on the census results?

A previous attempt at estimating observer bias in counting the number of whales in a group was made by Paul Sund of the Southwest Fisheries Center, NMFS (pers. comm.). In January 1977 he circled above migrating whales in a light aircraft (Cessna 172), and compared aerial counts with counts made by the observers at Granite Canyon for a total of 46 paired observations. While limited by small sample sizes, his results indicated the shore observer made a slight overestimate for single animals, and slight underestimates that increased with pod size for pods of two or more.

In an attempt to determine if a significant proportion of the population passes too far offshore to be seen, Rice and Wolman ran a transect in a small boat across the migration corridor on 18 January 1968. They began at Yankee Point and went to 37 kilometers offshore. Data from this single transect indicated that 24 of 33 whales sighted (73%) passed within 1.5 kilometers from the shore station (Rice and Wolman, 1971). Further, Sund and O'Connor (1974) reported estimated distances of 149 whales recorded off Monterey (Pt. Cypress to Pt. Sur) during January 1973. Their results agreed closely, indicating 94% within 1.6 kilometers.

Regarding diel variations in migration rate, Gilmore (1960) and Adams (1968) used arbitrary correction factors of 50% and 70%, respectively, to estimate nocturnal travel rates. Also, Hubbs and Hubbs (1967) as well as Ramsey (1968) believed there was some evidence of diel variation in rates. Cummings *et al.* (1968), IWC (1976 and 1977), and Rugh and Braham (1979) contrarily reported no apparent diel variations in migration rate. The data available for this study were examined for trends within the 10 hr (0700–1700) period of the censuses. Also, in an attempt to obtain further data on rate of passage at night, observation trails were made by Wolman with a Starlight Scope (1975; 1976), and night vision goggles (1977). Both were used under a variety of weather and lighting conditions. The binocular goggles do not magnify, but have a 40° field of view, in contrast to the monocular Starlight Scope which had only a 16° field of view. Very few whales were seen with either system. The few whales that were seen and tracked supported the hypothesis of animals moving at the same rate during night as they do during the daylight hours.

Direct measurement of observer biases. In order to test for bias in the observers' estimates of the numbers of animals in each group, and its distance offshore, it would ideally have been appropriate to have all past observers available for simultaneous experimental tests. The data recorded by each observer could then be corrected for that observer's individual biases. Since this was impossible, a group of 12 people (3 'experienced', 9 'naive') were used as a representative sample for such experiments.

At Granite Canyon on 30 and 31 December 1978, the 12 observers participated in the following experiments: For a total of 62 groups of whales passing offshore, each person made an independent estimate of distance to and number of individuals present in each pod. Simultaneously, Wolman circled above each group of whales in a Cessna 172 aircraft until an accurate count of the true number present was obtained. For a truth measure of the distance to each group, Reilly was positioned on a steep hill 200 m (660 ft) above and directly behind the census station, and used an inclinometer to measure the vertical angle to each group of whales as it passed directly offshore. From the angle, known elevation of the hilltop, and known distance to the water's edge, the distance of the whales from shore was calculated. The aircraft, census station, and inclinometer station were in radio contact to assure that they were all observing the same pod. Howard Braham coordinated the activity from the census station.

These experiments were conducted to measure bias *given* that a group of whales was sighted, which is equivalent to being recorded in past censuses. From these data, no estimates can be made of groups missed entirely.

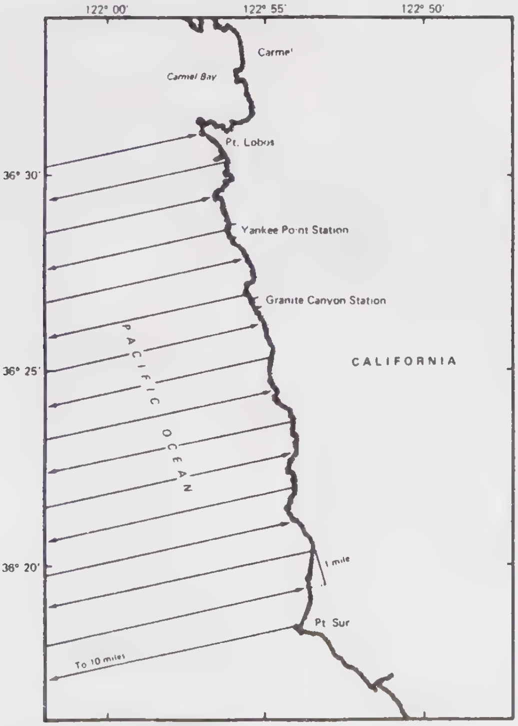

Fig. 1. Chart of California coast south of Monterey, showing census stations, and aerial transect lines.

Aerial transects of the migration corridor width. Flight transects were conducted to provide estimates of the corridor width, independent of the limited shore-based observers' estimates. Results from census studies based upon line transect and similar theory (Seber, 1973; Eberhardt, 1968, 1978) indicate that sighting efficiency decreases with increasing distance of an animal from the observer. A comparison of the observers' data on proportions of whales passing within each distance interval, with similar data from an 'unbiased' source should indicate the proportion of whales passing that are missed as a function of their distance from shore. A Cessna 172 aircraft flying at 300 m (1,000 feet) and 145 km/h (90 mph) altitude was used as this independent source. Although an observer in an aircraft will also miss a proportion of the whales passed over as a result of plane's elevation and speed, this proportion should be independent of the distance from shore. Consequently, while absolute counts from a plane will be biased, relative proportions of the total number seen per distance interval will be unbiased estimates of the true proportions, given sufficient sample sizes.

For this purpose a series of 16 transect lines were defined perpendicular to the coast at 1.6 km (1 mile) intervals between Point Sur and Point Lobos (Fig. 1). Each transect line extended from shore to 16 km (10 miles) at Sea.

Data from two previous shore censuses (1974/75 from Yankee Point; 1975/76 from Granite Canyon) were pooled, and used as a pre-sample of the proportions expected within each interval. The sample size requirement for the plane census was then determined by the formula (adapted from Cochran 1973):

$$N_T = \sum_{I=1}^{7} n_I = \sum_{I} \hat{p}_I \cdot \hat{q}_I \cdot (Z\alpha^2/d^2) \qquad (1)$$

where N_T = total sample required
n_I = sample required for interval I
$\hat{p}_I$ = estimate of the percent of the population in I from the past data
$\hat{q}_I$ = $(100 - \hat{p}_I)$
$Z\alpha$ = area under the normal curve for the required precision level
d = (100 − required precision level)

The method assumes that the estimates ($\hat{p}_I$) are normally distributed about the parametric values.

From (1) sample size requirements for 3 precision levels were determined (Table 2). Due to time and budgetary limitations, a 90 per cent precision level was accepted. Flights were continued until at least the minimum number of whales (330) assuring 90 per cent precision were recorded.

Table 2

Aerial transect sample size requirements for 3 levels of precision

	Precision level		
Number of	90%	92.5%	95%
Whales	330	582	1,311
Pods[a]	165	290	656

[a] Based upon an average approximately 2 per pod from pre-sample data.

Personnel for each flight included two observers and, when possible, a data recorder. On all flights, observations were also recorded on a cassette tape recorder through a microphone-headset system. Written data were verified by comparison with vocal data from the tapes.

The observer on each side of the plane concentrated on a 1.6 km (1 mile) strip of water, measured horizontally from the plane's track line by markings on the wing struts and windows. Left and right side duty were rotated between observers, and markings changed at each rotation to account for the different eye levels (and consequently different perspectives) of the observers.

Along each transect, whenever a group of whales was sighted within the one-mile strip, the number of animals was counted, and the elapsed time from the beginning of the transect to the moment when the animals were beneath the wing struts was recorded. The distance from shore was then calculated from the time difference between the sighting and the shore, and the plane's speed.

RESULTS

The Estimating Function

In its current state (June 1979) the estimating function begins with the ith estimate of the number of animals present in a sighting, (n_i). This estimate is then corrected for bias in estimating the true number present by the function $f(n_i)$, the computation of which is described below (eg. 8). Then for each jth day an average hourly rate is calculated. This is multiplied by 24 to produce an estimate for the entire day assuming a constant rate of migration throughout 24 hours. This daily estimate ($\hat{n}_j$) is then:

$$\hat{n}_j = (\Sigma f(n_i)/t_j)\cdot 24 \qquad (2)$$

where t_j is the total time watched on the jth day.
In equations 2–7, the notation is as follows:

n_i = original estimate of the number of animals present in the ith of observation,
$f(n_i)$ = the bias correction function for n – equation (8)
t_j = time watched during the jth day
$\hat{n}_j$ = number estimated for 24 hr day j corrected for bias in n_i = $[(\Sigma f(n_i)/t_j)\cdot 24]$
$\hat{p}_j$ = cumulative proportion of the population expected on the jth day,
$h(k)$ = bias correction for each year (kth) for proportion of whales missed offshore – equation (10)
$\hat{N}_j$ = estimate of the total population made on day j
$\hat{N}_l$ = estimate of the total population made on the last day of the census (j = l)

The next step is an estimation of the animals which pass by the station before and after the census period. This is done following a method developed to predict run size for migratory salmon (Mundy, 1979; Walters and Buckingham, 1975), in which a quantitative measure of the migratory timing is required: the cumulative proportion of the total 'run' expected on each day, calculated from past 'runs'. Their method basically, for each day j, estimates total population Nj by minimizing the least squares function

$$\Sigma_j (p_j - {}^{(\Sigma \hat{n}_j)}/_{N})^2 \qquad (3)$$

for N, according to Mundy (1979). This is solved for N by

$$\hat{N}_j = \Sigma_j(\Sigma \hat{n}_j)^2/(\Sigma \hat{n}_j \,.\, \hat{p}_j) \qquad (4)$$

Major assumptions of the method are that data fit a normal cumulative distribution, and that the mean days for each year are not significantly different. For our purposes, the only $\hat{N}_j$ of interest is that calculated on the last day of the census, $N_{j=l}$

Finally, the $\hat{N}_l$ is corrected for animals missed as a function of their distance from shore by the correction function h(k), for each year k. h(k) is a result of the differences between recorded and predicted (from aerial transects) proportions in the distance intervals (see equation (10) in Results section). The final estimating function is then:

$$\hat{N}_k = N_l \cdot h(k) \qquad (5)$$

The variance of N_k is estimated by the Delta Method, which is a Taylor series expansion with the higher order terms ignored (Seber 1973) as:

$$\text{est. Var}[\hat{N}_k] = \sum_{p=1}^{3} (\delta N_k/\delta x_p)^2 \cdot \text{Var}[x_p] + 2\Sigma\Sigma \,\text{cov}(x_p, x_q)\cdot[\delta N_k/\delta x_p]\cdot[\delta N_k/\delta x_q] \qquad (6)$$

where $x_1 = f(n_i)$; $x_2 = \hat{n}_j$; $x_3 = h(k)$.

Ninety-five percent confidence limits for the estimates are then:

$$\hat{N}_k \pm 1.96\sqrt{\text{Var}[N_k]} \qquad (7)$$

The Data Base

Data from 12 consecutive annual censuses near Monterey are currently under study. The latest of these, 1978/79, was not fully prepared for analysis in time for this report.

For developing a population estimate from the census results, the most important statistics are rate of animals recorded per unit time, and those statistics describing if and how this rate is affected by variability between observers, times of day, and visibility conditions. Three time units were examined: one hour, 5 hours (a ½ day observer shift) and 10 hours (a full day's watch).

1. *Animals recorded per 5-hour shift.* This was examined, within each census, for effects due to the observer on duty, the time of day (morning or afternoon) and average visibility code, by analysis of variance (ANOVA). Only periods which were exactly 5 hours were included in the analysis. There were differences between the two observers in only two censuses: 67/69 and 76/77. (F = 3.932, 3.908 respectively; data from these two censuses are currently under re-analysis to produce estimates which take these differences into account.) For the estimates produced in this report, data for the observers within each census are pooled. There were also no differences detected between periods with different visibility codes. This, however, could be a result of the elimination of periods shorter than 5 hours which were often those with bad visibility conditions. Another possible factor is that variability throughout the season resulting from the timing of the migration is probably great enough to overshadow any variability as a result of visibility. Consequently, this test is not conclusive, and further analysis is in progress.

This test does conclusively show that there were no differences between morning and afternoon periods in the numbers of animals recorded. Consequently, one-half day shifts were pooled for each day.

2. *Number of animals per hour of day.* Data for all censuses were pooled, then broken down into 10 one-hour groups (0700–1700), in order to test for indications of diel variation. Both an ANOVA of rate of animals recorded

per hour, with hours of day as groups (F = 1.608, d.f. = 9, ∞: n.s. at $\alpha = .05$) and a plot of average hourly rate by hour (Fig. 2) fail to indicate any change in migration rate during daylight hours. With no evidence to suggest that migration rate changes at night, a constant rate for each day is assumed here.

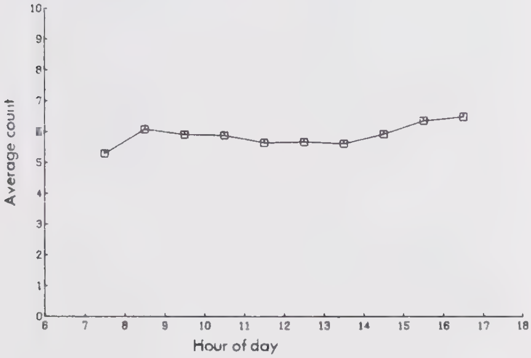

Fig. 2. Average number of gray whales recorded per hour at Monterey by hour of day for 0700–1700, from 11 annual censuses 1967/68–1977/78.

3. *Number of animals per 10-hour day.* The average hourly rate recorded per day is used as a basis for extrapolation over 24 hours for each day. The average hourly rate is used rather than the days sum to account for days in which less than 10 hours were watched.

4. *The migratory corridor: differences between locations.* In order to determine if the move to Granite Canyon in 1975/76 has had an effect on census results, data from each location were pooled, and broken down into relative proportions recorded within the seven intervals of distance from shore. A difference in the distances of animals from shore between the two locations could result in higher or lower counts. Table 3 lists a Chi-squared contingency test of differences between proportions per interval at the two locations. They are not significantly different at $\alpha = .05$. (Similarly, a t-test of differences in mean distance indicated no difference.) Consequently location difference between early and late censuses is not considered an important factor at this time.

5. *The migratory corridor: changes during each migration.* As we were only able to conduct verification experiments on the migratory corridor during the middle third of the migration, the census results were tested for possible differences in distances of animals from shore during the migration. Data were divided into three approximately equal time segments: 'early' = 10 Dec–29 Dec; 'mid' = 30 Dec–18 Jan; 'late' = 19 Jan–6 Feb. While a χ^2 test of differences in proportions between the midseason results and those for the early and late seasonal periods indicated no significant differences (early $\chi^2 = 4.55$. Late $\chi^2 = 11.78$; compared to $\chi_{6,.05} = 12.592$) an ANOVA of mean distances of the three seasonal groups indicated they were significantly different (Table 4). A multiple classification analysis (Nie *et al.* 1975) indicates that early and late seasons are not different, but together they are different from the midseason, the whales being recorded farther from shore, on average, at that time. As there was a disagreement between test results, the conservative route was chosen, and only the mid-season data used for comparison with results from aerial transects of the migration corridor.

Table 3

Chi squared contingency test for differences in proportions of observations per offshore interval between Yankee Point and Granite Canyon

Distance increment	Yankee Point (8 yrs)	Granite Canyon (3 yrs)
0. –0.25	31.7	46.5
0.25–0.5	34.7	29.4
0.5 –0.75	15.9	12.2
0.75–1.0	11.5	7.1
1.0 –1.5	3.8	2.8
1.5 –2.0	1.8	1.6
2.0+	0.6	0.4

$\chi^2 = 10.567$ not significant at $\alpha = .05$.
$\chi^2_{.05,6} = 12.592$.

Table 4

ANOVA of distance of observations from shore, with early, middle and late season as groups

Season	$\bar{X}$	SD	n
Early	.5093	.3302	3,980
Mid	.5897	.4357	10,616
Late	.4825	.3835	4,878
All	.5463	.4076	19,474

Source of variation	DF	Mean square	F
Between groups	2	15.2284	92.9788**
Within groups	19,472	0.1638	

** Significant at $\alpha = .01$.

The Verification Experiments

1. *Estimation of the number of whales present in each group.* Data for this experiment were collected over the course of two days, involving estimates for 62 groups of whales. The observations from the first morning (12) were thrown out, being considered an orientation exercise. Of the remaining 50, the plane was present to make a truth count for 34. In these a total of 381 estimates were recorded. An analysis of variance of errors in estimating the true number of whales present per group with people (12) and true number (4) as groups (Table 5) shows that both factors are significant, as is the interaction between them. That is, there were significant differences between observers not only in their overall bias, but in their relative biases for each group size. Also, overall, there are

Table 5

Analysis of variance for errors in estimating the number of whales present per observation with observers (12) and pod sizes (4) as groups.

Source	SS	DF	MS	F
Mean	169.088	1	169.088	(74.700)
People	85.796	11	7.799	3.446**
Group size	137.717	3	45.905	20.281**
People × group size	165.629	33	5.019	2.217**
Error	785.449	347	2.263	
Total	1,343.449	395		

** Significant at $\alpha = .01$.

differences in bias for different numbers of whales per group. An estimation of the average bias for each estimate n, was calculated as (bias of n) = (estimated number (n) − ave. true number). As indicated in Table 6, estimates of 1 and 4 or more were significantly below the true value, while those for 2 and 3 were not significantly different from the true values.

To correct past data for this measured bias, the function f(n) is defined

$$E[n] = f(n) = n + b_n = \begin{cases} n + .350 & n = 1 \\ n + 0 & n = 2, 3 \\ n + .333 & n \geq 4 \end{cases} \qquad (8)$$

with variance estimated as

$$\mathrm{Var}[f(n)] = \begin{matrix} .464 \\ 0 \\ \cancel{.333} \\ .612 \end{matrix} \begin{cases} n = 1 \\ n = 2, 3 \\ n \geq 4 \end{cases} \qquad (9)$$

Table 6

Bias of estimates of numbers present per observation, from 1973 verification experiment

Estimate	$\bar{X}$ Truth count	Standard deviation	n	t	Bias
1	1.350	0.6812	225	7.709*	−0.350
2	2.178	0.9316	101	1.921	0
3	3.035	1.290	28	0.144	0
4 or more[a]		0.7825	27	2.210*	−0.333

* Significant at $\alpha = .05$.

[a] The data for observations of 4 or more were compared individually to their true counts. The 'bias' listed above is the average residual of these 27 observations.

Table 7

Analysis of variance for errors in estimating the true distance interval in which a group of whales passes, with people (12) and true intervals (4) as groups

Source	SS	DF	MS	F
People	238.664	11	21.696	13.839*
True interval	22.338	4	5.585	3.562*
People × true interval	132.514	44	3.012	1.921*
Error	755.679	482	1.568	
Total	1,149.195	572		

* Significant at $\alpha = .05$.

2. *Estimation of distances of groups of whales from shore.* After an initial orientation period, 542 estimates were made for 50 occurrences of whales passing offshore. For each of these 50 there was an inclinometer truth measurement taken. Data from both the estimates and the truth measurements were classified into the seven distance intervals. An analysis of variance of errors in estimating the true distance interval in which a pod of whales is passing, with people (12) and true interval (4) as groups (Table 7) shows that both factors are significant, as is the interaction (just as with number estimation). That is, not only are people different in their ability to accurately estimate distances, but they differ also in where they make significant errors in estimating distances. Table 8 lists the average true distance for estimates of each of the seven intervals. For all intervals except 1–1.5 miles the true interval was on average significantly different from that estimated. Both within the area from shore to 1 mile out, and within the area beyond 1.5 miles, there are serious

Table 8

Results of distance estimation bias experiments from Granite Canyon 30, 31 December 1978

Estimated distance	1 (0–.25)	2 (25–.5)	3 (.5–.75)	4 (.75–1.0)	5 (1.0–1.5)	6 (1.5–2.0)	7 (2.0+)
Number of observations	18	55	101	183	114	47	24
Relative frequency	.033	.101	.186	.337	.210	.086	.04
Average true distance	0.556	0.683	0.871	0.995	1.250	1.350	1.208
Sd	0.137	0.244	0.303	0.259	0.306	0.371	0.319
t	13.385*	11.397*	8.159*	6.267*	0	7.392*	12.285*

* Significant at $\alpha = .05$.

Table 9

Data from aerial transects of migrating gray whales between Point Sur and Point Lobos, California during January 1979

Number	Date	Elapsed air time (hr)	Number of observations	Number of animals	Comments
1	2 Jan 79	3:00	16	27	200 + *Grampus;* 50–75 sea lions; 3–10 unident. porpoise
2	4 Jan 79	2:52	18	31	
3	4 Jan 79	2:55	26	45	
4	5 Jan 79	2:40	25	46	130 *Grampus;* 50+ *Phocoenoides*
5	6 Jan 79	2:35	26	40	80+ unident. porpoise
6	6 Jan 79	2:42	28	66	12 *Grampus;* 80± unident. porpoise
7	7 Jan 79	1:24	5	99	5 *Phocoenoides*
8	9 Jan 79	0:55	3	4	abort due to poor visibility: wind and chop
9	9 Jan 79	1:00	0	0	abort due to fog
10	10 Jan 79	2:20	21	36	2 *Phocoenoides*
11	12 Jan 79	1:00	0	0	abort due to equipt. malfunction
12	12 Jan 79	2:47	21	38	50+ *Grampus*
13	13 Jan 79	2:37	22	57	10± 2 sea lion; 8 unident. porpoise; 15 *Lagenorhynchus*
14	13 Jan 79	2:52	20	40	100+ *Lagenorhynchus;* 2 *Zalophus;* mixed group stellar sea lions (50+) and *Lagenorhynchus* (75+)

misclassification problems. Unfortunately during the experimental period, no whales actually passed within the closest and farthest intervals (1, 7).

3. Aerial estimation of the migration corridor. A total of 14 flights were taken during the period 2 January 1979 and 13 January 1979 (Table 9). Of these, two were aborted before actually beginning the transects (9, 11) and two others were aborted after only a few legs (8, 10). In general, data were collected during periods of 'good' to 'excellent' visibility.

Data on distances of whales from shore were examined for effect of side of planes and leg number (1–16), while data on number of whales sighted were examined for effects of observer, side of plane, and morning vs. afternoon flight.

Table 10

ANOVA of estimated distance of whales from the airplane, with sides of plane and transects legs as groups (raw data)

Source	SS	DF	MS	F
Sides	1.886	1	1.886	7.7*
Legs	26.106	15	1.740	7.1*
Sides × legs	14.985	15	0.999	4.1*
Error	94.186	384	0.245	

* Significant at $\alpha = .05$.

An ANOVA of distance estimates with side of plane and legs as groups (Table 10) indicates that both factors are significant. The differences between sides is to be expected, as the person on the left sat behind the pilot, while the person on right sat next to the pilot, resulting in differing perspectives for identifying the time at which the wing strut passed over an object. In fact, the mean distance estimates for the two sides (1.405 miles left; 1.205 miles right) are different by exactly 0.2 miles, which corresponds to 8 seconds of flight at 90 mph. To account for this difference, left side estimates were adjusted by −0.2 miles (−8 sec), under the assumption that right side estimates were accurate, as that side afforded the greater visibility. A second ANOVA (Table 11), with these adjusted data, shows no significant difference between sides. Data were consequently pooled from both sides. The differences between legs are possibly due to very small samples per leg (in fact only when all legs are pooled are there enough data for even 90 per cent precision). Another possibility is that the whales are responding to the relatively slight variations in coastal geography along the stretch of coast surveyed. As there aren't sufficient observations per leg to test this quantitatively, a qualitative examination of the location of observations in relation to varying bottom contours is in progress. For the present, data from all legs are pooled.

Table 11

ANOVA of estimated distances of whales from the airplane, with sides of plane and transect legs as groups (left side data adjusted by −.2 mi)

Source	SS	DF	MS	F
Sides	0.1155	1	.116	0.5 n.s.
Legs	26.106	15	1.740	7.1*
Sides × legs	14.985	15	0.999	4.1*
Error	94.186	384	0.295	

* Significant at $\alpha = .05$.

Flight data on number of whales sighted per flight were examined by factorial ANOVA for differences in sighting efficiency due to observer (skill), side of plane and morning vs afternoon flights (Table 12). There were no significant differences due to these factors, indicating that over 14 flights, neither differences in observers, side of plane or time of day significantly affected this aspect of the plane census results.

Table 12

ANOVA of number of whales sighted per flight during aerial transects of the gray whale migration corridor, 2–13 January 1979. Groups are sides of plane, observers, and period (morning vs afternoon)

Source	SS	DF	MS	F[a]
Sides	63.375	1	63.375	0.5
Observers	117.042	1	117.042	1.0
Sides × observers	155.042	1	155.042	1.3
Periods	57.042	1	57.042	0.5
Sides × periods	9.375	1	9.375	0.1
Observers × periods	126.042	1	126.042	1.1
Sides × observers periods	45.375	1	45.917	0.4
Error	1886.667	16		

[a] None significant at $\alpha = .05$.

Table 13

Relative and cumulative frequencies of observations in distance increments for the mid-season (29/12–18/01). 11 years. Compared to 'best estimate' from aerial transects

Distance interval		Plane transect predicted	67/68	68/69	69/70	70/71	71/72	72/73	73/74	74/75	75/76	76/77	77/78
1	rel.	3.4%	29.7	40.5	27.6	28.0	14.4	15.6	25.6	13.3	51.8	49.1	62.8
	cum.	(3.4)	(29.7)	(40.5)	(27.6)	(28.0)	(14.4)	(15.6)	(25.6)	(13.3)	(51.8)	(49.1)	(62.8)
2		8.7	37.6	49.4	36.7	31.7	27.6	35.5	25.9	17.9	29.9	35.0	25.8
		(12.1)	(67.3)	(89.9)	(64.3)	(59.7)	(42.0)	(51.1)	(51.5)	(31.2)	(81.7)	(84.1)	(88.6)
3		9.9	17.2	5.1	23.1	23.9	14.9	25.1	18.9	21.6	11.6	11.4	7.5
		(22.0)	(84.5)	(95.0)	(87.4)	(33.6)	(56.9)	(76.2)	(70.4)	(52.3)	(93.3)	(95.5)	(96.1)
4		17.3	7.6	4.4	7.8	11.1	27.4	13.8	19.0	24.4	4.8	3.1	2.8
		(39.3)	(92.1)	(98.0)	(95.2)	(94.7)	(84.3)	(90.0)	(89.4)	(77.2)	(98.1)	(98.6)	(98.9)
5		35.6	2.8	0.5	2.4	2.9	14.0	4.9	5.5	12.5	1.1	1.0	1.0
		(75.4)	(94.9)	(99.5)	(97.6)	(97.6)	(98.3)	(94.9)	(94.9)	(89.7)	(99.2)	(99.6)	100.0
6		17.08	3.0	0.0	0.2	1.9	1.1	3.7	3.9	8.0	0.7	0.5	0.0
		(93.2)	(97.9)	(99.1)	(97.8)	(99.5)	(99.3)	(98.6)	(98.9)	(97.7)	(99.9)	(100.0)	0.0
7		7.0	2.1	0.1	0.1	0.5	0.7	1.4	1.1	2.4	0.1	0.0	0.0
		(100.0)	(100.0)	(99.6)	(97.9)	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	0.0	0.0

All aerial data pooled, broken down into proportions within the seven distance increments, were compared with the same data from the midseason (30 Dec–10 Jan) of each individual census (Table 13). Chi-squared tests indicate that all years are significantly different from the aerial predictions ($X^2 > 300$ for all : $\alpha = 0.1$). (Significant differences beyond 90 per cent are not meaningful here, as this was the sampling efficiency of the aerial census).

An estimator of the function h(k) (see methods section) from both the misclassification bias and from the differences between predicted and observed corridor distance interval proportions is in progress. At present, as a temporary approximator, data are pooled in two classes: 'inshore' (from shore to 1.5 miles), and 'offshore' (beyond 1.5 miles). Justification for the break at 1.5 miles comes from misclassification bias being a significant problem on both sides of the interval 1–1.5 miles, while there is no apparent bias within this interval. A necessary assumption is that in the 'inshore distance interval, virtually all groups of whales that passed were sighted. A simple function, then, for each year (k) is:

$$h(k) = C_p/c_s \qquad (10)$$

where C_p = cumulative proportion inshore predicted from aerial censuses

c_s = cumulative proportion inshore observed for the year h

The variance of h (k) is estimated by the Delta method (Seber, 1973) as:

$$\text{est. Var}\,[h(k)] = [-C_p/c_s{}^2]^2\text{Var}[C_p] + (1/C_p)^2\text{Var}[s_s] \qquad (11)$$

$$\text{where Var}[C_p] = (C_p).(1-C_p)/n_p \qquad (12)$$

$$\text{and Var}\,[c_s] = (c_s).(1-c_s)/n_s \qquad (13)$$

Values of h (k) are listed in Table 14.

Table 14

Values estimated for the correcting function h(k), for k = 1, 11

Year	h(k)
1967/68	1.26
1968/69	1.32
1969/70	1.29
1970/71	1.29
1971/72	1.31
1972/73	1.26
1973/74	1.26
1974/75	1.19
1975/76	1.31
1976/77	1.32
1977/78	1.33
1978/79	1.29

Migratory timing and estimation of whales passing following the census

The cumulative proportions of the whales seen each day during the period 10 Dec–6 Feb (all years combined) as fit by the cumulative normal (estimated by the logistic) are shown in Fig. 3 (taken from Table 15). As the fit is very good the major assumption of equality of mean days over years is however, not met by the data (median test $T = 2{,}745 \times {}^{2}10_{j}{,}05$). As the effect of this violation on the final population estimate is minor, the adjustment for migration tails was conducted assuming equality.

Table 15

Monterey gray whale census. Number of animals sighted per day (adjusted number—see text), relative frequency (adj) and cumulative frequency (adj)

Date	Adjusted count	Per cent	Cumulative per cent
1 10 Dec	12.905	.13	.13
2 11 Dec	21.563	.21	.33
3 12 Dec	30.953	.30	.63
4 13 Dec	37.286	.36	.1.00
5 14 Dec	44.804	.43	1.43
6 15 Dec	47.772	.46	.1.89
7 16 Dec	45.397	.44	.2.33
8 17 Dec	46.495	.45	.2.78
9 18 Dec	65.217	.63	3.42
10 19 Dec	76.887	.75	4.16
11 20 Dec	84.739	.82	4.98
12 21 Dec	83.784	.81	5.79
13 22 Dec	117.214	1.14	6.93
14 23 Dec	143.658	1.39	8.32
15 24 Dec	150.503	1.46	9.78
16 25 Dec	151.203	1.47	11.25
17 26 Dec	161.880	1.57	12.82
18 27 Dec	207.556	2.01	14.83
19 28 Dec	205.425	1.99	16.82
20 29 Dec	185.356	1.80	18.62
21 30 Dec	224.817	2.18	20.80
22 31 Dec	280.459	2.72	23.52
23 1 Jan	290.003	2.81	26.53
24 2 Jan	284.557	2.76	29.09
25 3 Jan	363.821	3.53	32.61
26 4 Jan	420.755	4.08	36.69
27 5 Jan	371.890	3.60	40.30
28 6 Jan	402.371	3.90	44.20
29 7 Jan	382.179	3.70	47.90
30 8 Jan	287.085	2.78	50.68
31 9 Jan	276.636	2.68	53.37
32 10 Jan	333.840	3.24	56.60
33 11 Jan	314.091	3.04	59.65
34 12 Jan	278.278	2.70	62.34
35 13 Jan	303.374	2.94	65.28
36 14 Jan	271.297	2.63	67.91
37 15 Jan	254.513	2.47	70.38
38 16 Jan	235.295	2.28	72.66
39 17 Jan	247.296	2.40	75.06
40 18 Jan	190.440	1.85	76.91
41 19 Jan	215.155	2.09	78.99
42 20 Jan	204.857	1.99	80.98
43 21 Jan	213.319	2.07	83.04
44 22 Jan	198.859	1.93	84.97
45 23 Jan	197.393	1.91	86.89
46 24 Jan	162.597	1.58	85.46
47 25 Jan	158.802	1.54	90.00
48 26 Jan	149.114	1.45	91.45
49 27 Jan	149.140	1.45	92.89
50 28 Jan	125.544	1.22	94.11
51 29 Jan	23.427	.23	94.34
52 30 Jan	91.619	.89	95.22
53 31 Jan	82.017	.80	96.02
54 1 Feb	81.478	.79	96.81
55 2 Feb	71.358	.69	97.50
56 3 Feb	45.740	.44	97.95
57 4 Feb	47.491	.46	98.41
58 5 Feb	30.714	.30	98.71
59 6 Feb	36.534	.35	99.06

Mean day = 31.
Variance = 137.89.

Table 16 lists values of the original counts ($\Sigma\, n_i$), counts adjusted for 24 hours and whales missed per pod seen ($\Sigma\, \hat{n}_j$), and the $\Sigma\, \hat{n}_j$ adjusted for whales passing after the census ($\hat{N}_i$). The average numbers of animals seen per day over the eleven years are plotted in Fig. 4.

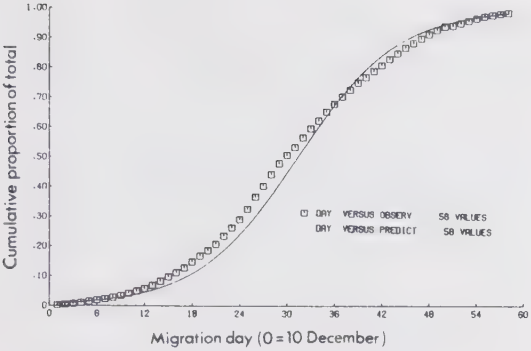

Fig. 3. Cumulative proportion of total count by day for 11 years (averaged) fit to the logistic, as an approximation to the cumulative normal.

Table 16

Sums of daily counts. Σn_i = raw data. $\Sigma \hat{n}_i$ = raw data adjusted for 24 hour and number estimate bias; $\hat{N}_i$ = adjusted for tails of migration

Year	Σn_i	Σn_i	$\hat{N}_i$
67/68	3,077	8,373	8,545
68/69	3,265	8,514	8,624
69/70	3,399	8,990	9,107
70/71	3,264	8,605	8,717
71/72	2,667	7,248	7,357
72/73	3,684	10,316	10,450
73/74	3,889	10,193	10,325
74/75	3,836	10,012	10,142
75/76	4,295	11,165	11,397
76/77	4,720	12,348	12,508
77/78	3,717	10,106	10,259
78/79	3,927	10,317	10,450

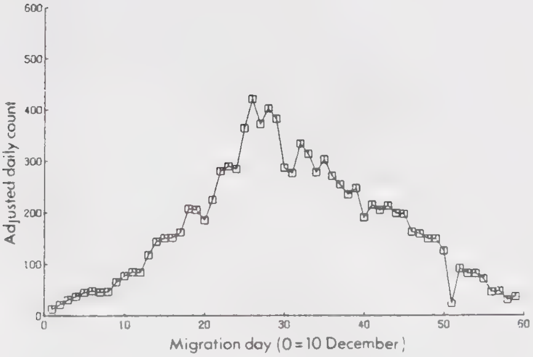

Fig. 4. Average daily counts of gray whales from Monterey, California, 1967/68–1977/78. Counts are adjusted for number estimation bias, and for the full 24 hour day.

Final estimates and their variances

Final estimates for each census are obtained by multiplying N_i by h(k) to complete the entire estimation process (as of this date).

The final form of the variance equation for the population estimator (Var[N_k]) was computed with the assumption that the covariances (6) were zero.

Table 17

Estimates of the population size of the California stock of the gray whale, and their variances and confidence limits, from 11 consecutive annual censuses at Monterey, California

Year	Estimate ($\hat{N}_k$)	Var [$\hat{N}_k$]	C.I.
1967/68	10,767	1,034,843	(8,773, 12,761)
1968/69	11,384	1,214,051	(9,224, 13,544)
1969/70	11,748	1,223,782	(9,579, 13,916)
1970/71	11,245	1,198,525	(9,099, 13,390)
1971/72	9,637	831,332	(7,851, 11,424)
1972/73	13,167	1,516,403	(10,753, 15,581)
1973/74	13,010	1,501,919	(10,608, 15,412)
1974/75	12,069	1,411,499	(9,746, 14,398)
1975/76	14,930	1,777,799	(12,316, 17,543)
1976/77	16,511	2,163,435	(13,628, 19,394)
1977/78	13,644	1,550,369	(11,204, 16,084)
1978/79	13,460	1,525,210	(11,039, 15,880)

CONCLUSIONS

Table 17 lists the final estimates, their variances and 95 per cent confidence limits.

The population estimates presented here must be considered tentative until such time as: (1) the function correcting for whales offshore as a result of the aerial transect results (h(k)) can be estimated more accurately; (2) night travel rates can be more accurately substantiated; and most importantly (3) the effects of variability of weather (visibility) conditions on census results can be quantified in some form. Research is in progress on all 3 areas.

These estimates are most likely below the actual values, since no correction has been made for poor visibility (which certainly has an effect on an observer's ability to accurately census passing whales) and because the approximation to h(k) used here is the most conservative reasonably possible at this time. Consequently, the highest estimate produced (16,511 for 1976/77) is probably the best estimate available at this time. Further, that year was a 'drought' year in California, with an exceptionally clear and stormless winter, during which weather variability would be expected to be low.

The very lowest estimate (9,637 in 1971/72) came from a year which reportedly was 'stormier than usual', and its low value could be due to this in part.

While no attempt has been made to fit a line through the estimates presented, there is some indication that the population has been increasing during the period from 1967 to 1978. When the data from 1979/80 are analyzed, this estimate (in addition to the quantification of visibility) should help to define any trends which have possibly occurred in population size.

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8074

A Review of Studies to 1970 of Growth Layers in the Teeth of Marine Mammals

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ABSTRACT

This is a review of the discoveries of layers in teeth of marine mammals and subsequent researches that led to the widespread use of dental layers for age determination of marine mammals. Zoologists during the 19th century noted the existence of layers in marine mammal teeth, but it remained for Boschma, in 1938, to associate dental layers with age, and Chapskii, in 1941, to recognize the value of layers to wildlife research. Methods for aging and analyzing samples from marine mammal populations were developed in the early 1950s and have since been applied to most extant species of toothed marine mammals. A systematic account of the first 40 years of age determination research on 36 species of Cetacea, Pinnipedia, and Sirenia, is presented.

INTRODUCTION

> In the central blinds of bone, as they stand in their natural order, there are certain curious marks, curves, hollows, and ridges, whereby some whale-men calculate the creature's age, as the age of an oak by its circular rings. Though the certainty of this criterion is far from demonstrable, yet it has the savor of analogical probability.
> (Melville, 1851, p. 324)

Age composition is one of the life history parameters needed to assess the dynamics of mammalian populations. In the past, criteria such as body length, eye lens weight, degree of closure of cranial sutures, tooth wear, and the number of corpora albicantia have been used to estimate *physiological age* in many species. For marine mammals, growth layers deposited in the teeth are a more useful criterion because they indicate *chronological age*. Tooth-age determination has become standard procedure in stock assessment and management decisions for marine mammals. This paper is an account of the pioneering efforts and progress up to 1970 in estimating the age of marine mammals by counting dental layers.

HISTORICAL SUMMARY

Zoologists of the 19th century described or illustrated growth layers in teeth of marine mammals without seeming to understand their significance. Owen (1845) and Eschricht (1845, 1862) mentioned concentric layers in teeth of odontocetes. Witness also the sketches of a beaked whale tooth in Lankester's 1867 paper and the delicate lithographs of sperm whale and killer whale teeth in Van Beneden and Gervais' 1880 monograph (plates 20 and 49). The first person to correlate growth layers with age in years was Boschma, who in the late 1930s examined a longitudinal section of a sperm whale tooth.

Chapskii, in 1941, was among the first to foresee the value in wildlife research of counting layers. Through examination of cross sections of walrus premolars he estimated ages up to 27 years. The value of growth layers was recognized in 1948 by Scheffer (1950), who developed a technique for aging otariids. In the same year, Laws (1952), studying elephant seal teeth from South Georgia, developed a technique for aging phocids. In his 1952 paper, Laws stated that

> a superficial examination of material in museums indicates that the teeth of a number of other vertebrates, living and fossil, have internal rings or external ridges which, like those found in seals, may possibly be used for determining age (p. 974).

Nishiwaki and Yagi (1953) were first to use dental layers in determining age of cetaceans. After the early 1950s, research using this method of age determination increased rapidly, and by the late 1960s the method had been applied to most species of toothed sea mammals.

SYSTEMATIC ACCOUNT

(Terminology follows IWC recommendations)

Cetacea: Physeteridae

Physeter macrocephalus **(sperm whale)**
Boschma (1938) made a thorough study of the teeth of the sperm whale (our Fig. 1). He examined polished, longitudinal sections of a tooth from the Antarctic and was struck with the regular distribution of osteodentinal 'pearls' parallel to, and sandwiched between, the layers of orthodentin (p. 243). He likened the series to the 'winter-rings in the scales of fishes' and surmised that the animal must have been at least seven years old.

Nishiwaki *et al* (1958) made the first intensive study of growth zones in sperm whale teeth. In 40 whales, they found 21 to 28 teeth in each lower quadrant. In 27 of the whales, there were no visible upper teeth; in five there were from two to thirteen visible upper teeth, and in eight the presence of upper teeth was uncertain or unrecorded. The authors studied teeth numbers seven to ten in the lower series, the largest. They took teeth from 37 males and 51 females. With saw, rasp, and grindstone they made longitudinal sections and counted 'laminations' in the dentine. Laminations in the cementum were often worn or obscure, and were not

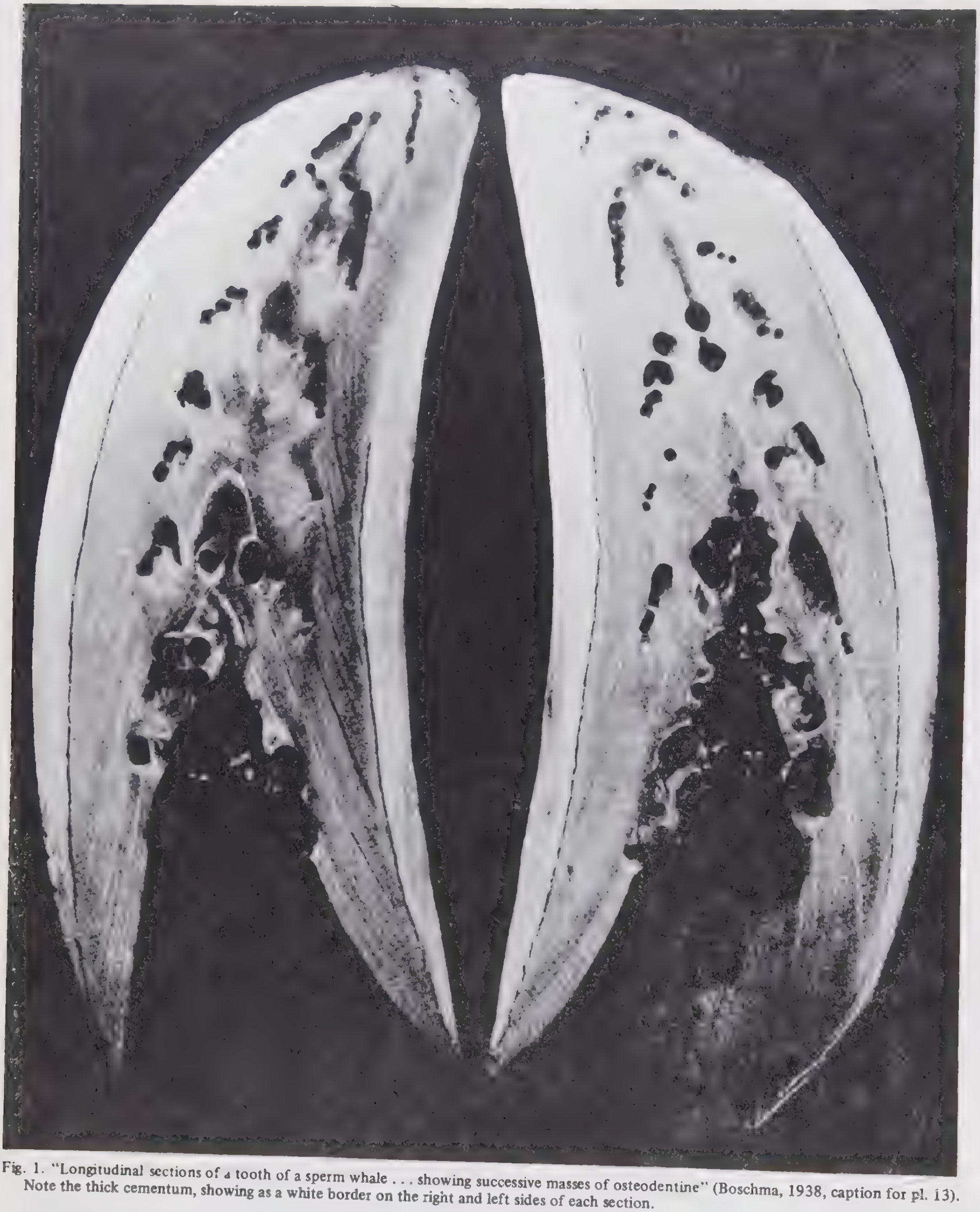

Fig. 1. "Longitudinal sections of a tooth of a sperm whale . . . showing successive masses of osteodentine" (Boschma, 1938, caption for pl. 13). Note the thick cementum, showing as a white border on the right and left sides of each section.

useful indicators of age. The authors concluded tentatively that two laminations are laid down in dentin each year. On this basis, males, with up to 48 laminations, should attain sexual maturity at age four or five years, with nine or ten laminations. Females, with up to 70 laminations, should attain sexual maturity at age four. A 'lamination' as used here is a seasonal zone, and two zones make an annual layer. Ohsumi *et al* (1963) were later to show that one layer, consisting of a dark and a light zone, is deposited annually.

In material from 24 sperm whales, Nishiwaki *et al* (1961) studied the relationship between the number of layers in mandibular bone and in teeth. Layering in bone does not present a permanent record.

As the bone tissue is resorbed from the mandibular

> canal, the laminations will disappear at different rates according to the positions on the mandible (p.502).

Layers are most persistent near the middle of the mandible, behind the symphysis. In females there is evidently a one-to-one relationship between the number of layers in bone and dentin until the period when about 13 layers have been formed. Thereafter the number in the bone remains constant at about 14, while that in the dentin continues to increase. Although the authors had jaws from only three adult males, with 14 or 15 bone layers, they stated that

> 18 laminations were observed in a mandible of an Antarctic male sperm whale, so it is probable that more laminations remain in the male than in the female (p. 503).

Berzin (1961a) reported that

> the age was determined from the teeth in 306 male and 61 female sperm whales. Assuming the annual deposition of two layers of dentin in the teeth (winter and summer), it can be calculated that the males reach sexual maturity at an age of four and a half to five years and a body length of 9.5 m to 10 m. The seventh and ninth pairs of teeth are the first to be cut, while the front and back are the last (at ten to eleven years). The pulp cavity of the first pair becomes filled in at the age of 30 to 35 years. The similarity in calcification of the two layers (winter and summer) indicates that the sperm whale does not have a prolonged winter fast . . . (p. 17279).

The oldest males and females were 28 to 32 years old, respectively.

Berzin (1961b) reported further details of his study of the 61 females. In sexually mature animals four to five years old or older he found one 'corpus luteum vestige' [corpus albicans] for each two layers of dentin. This relationship confirmed his opinion that two layers are deposited annually. In older females, however, the age estimated from tooth layers was greater than that estimated from corpora, from which he concluded that the cycle of ovulation is interrupted from time to time in older whales. The oldest specimen was 'barren', age 29 from the evidence of the ovaries and age 30-plus from the evidence of the teeth.

Omura *et al* (1962) described the skeleton of a male sperm whale 46 feet long. The animal was evidently not fully grown; the vertebral epiphyses were not completely ankylosed. The authors stated that 'the body length of male sperm whales at the attainment of physical maturity is thought to be between 52 and 53 feet' (p. 36). A longitudinal section of an upper tooth of this animal showed '32 laminae'.

Laws (1962, Fig. 8) reproduced a photograph of a thin longitudinal section of a lower tooth with '36 incremental layers' in dentin and cementum (representing about 18 years). The cementum layers show exceptionally well in this figure.

Ohsumi *et al* (1963) used maxillary teeth of the sperm whale in a study of growth layers. Most of the maxillary teeth, similar in the two sexes, remain hidden in the gum through life where they are protected from wear and damage. The authors saved one buried tooth from near the middle of an upper tooth row from each of 448 whales taken in the North Pacific in 1960–61. They also studied the teeth of eight whales which were marked in 1952–60 and recovered in 1962. In longitudinal sections the important layers were:

(1) the forming layer, next to the pulp, consisting of predentin and dentin, and

(2) the next-oldest layer, i.e. the one of the preceding season (our Fig. 2).

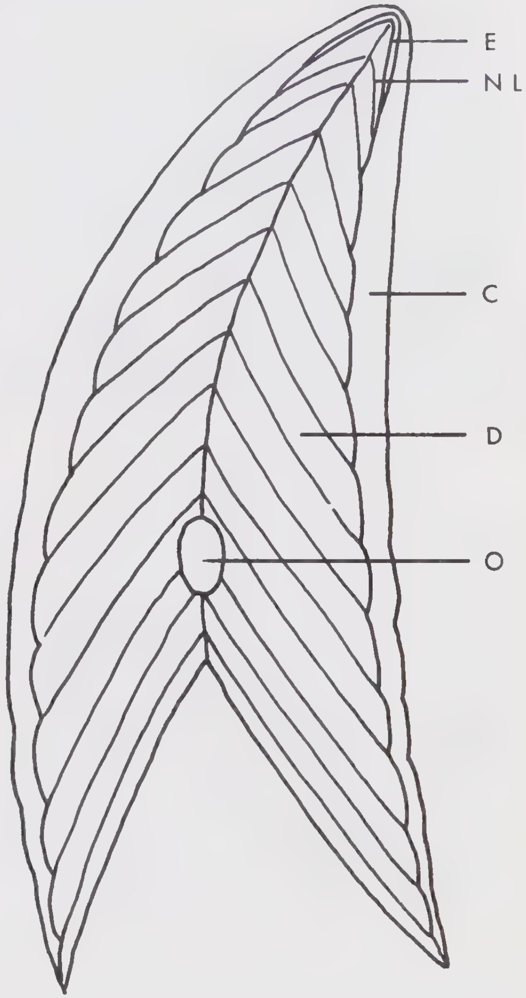

Fig. 2. Diagram of an unerupted maxillary tooth of an adult sperm whale; longitudinal section. E = enamel, representing a very small portion of the tooth, NL = neonatal line, C = cementum, D = dentine, O = osteodentin. (After Ohsumi *et al.*, 1963, Fig. 1).

A 'layer' was defined as the zone between narrow 'dark bands'.

The dark and light layers are seen by reflected light as translucent and opaque layers by transmitted light. Since the translucent layer is anisotropic in polarized light and is weakly stained by carbol-fuchsin, the authors concluded that it has a better developed crystalline structure than the thick opaque layer.

With increasing age, the thickness of the newest layer tends to decrease. Mean layer thickness in males is slightly greater than in females. In the authors' sample, the mean number of layers in males was 18.7 (5 to 35) and in females 14.4 (4 to 27).

By plotting the distance between the latest dark layer and the pulp against the date of capture, the authors deduced that the dark layer is laid down in midwinter, or January. In certain individuals, however, the layer may begin to form as early as mid-October and in others it may not be completed until April. 'The dark band [layer] . . . seems to be accumulated as the result of a good nutritious condition' (p.32).

Partly from these measurements of seasonal progression in thickness of dentin and partly from study of marked whales, the authors concluded that only one dark layer a year is deposited. A female about 37 feet long was marked at sea on 17 June 1953 and killed on 30 August 1961, when her length was verified as 35 feet. An upper tooth showed 14 layers and her ovaries two corpora albicantia. The evidence fits the assumption that she was nearly adult when marked (6 years, 6 layers) and fully adult when killed (14 years, 14 layers).

Gambell and Grzegorzewska (1967), using a sample of mandibular teeth from 659 sperm whales from South American and Antarctic waters, analyzed the rate of layer formation. They concluded that a layer containing a light and a dark band was laid down twice a year.

Cetacea: Monodontidae

***Delphinapterus leucas* (white whale)**
Yablokov (1958, pp. 41–3) figured the teeth of the white whale but did not discuss growth layers.

Sergeant (1959) examined teeth of several hundred white whales taken in the northeastern Canadian Arctic. He made longitudinal thin sections and counted up to 50 layers in the dentin. He tentatively concluded that two complete layers (four zones) are deposited yearly.

The relationship between layers and age is still unclear (Sergeant, 1962a, p. 4).

> Soviet workers, on the basis of length-frequencies, believe beluga to become white in colour and the females to mature sexually as early as the third year, males in the fourth. The discovery of growth-layers in the teeth has begun to allow accurate age determination; but the rate of deposition of the layers, and hence the absolute age which they represent, has not yet been determined.

Cetacea: Ziphiidae

***Berardius bairdii* (Baird's beaked whale)**
Omura *et al* (1955, p. 107) illustrated a longitudinal section of a tooth of a Baird's beaked whale and suggested the possibility of estimating age by growth layers (our Fig. 3).

The anterior teeth are peculiar in that the pulp cavity becomes filled with osteodentin and very little orthodentin.

> Outside the teeth a layer of cement is formed yearly, making a coating of cement from which, we think, it is possible to determine the age (p. 107).

There appear to be four layers of cementum on the tooth illustrated.

Yablokov (1958, Fig. 5) illustrated a longitudinal section of a *Berardius* tooth but did not show growth layers.

***Mesoplodon bidens* (Sowerby's beaked whale)**
Lankester (1867, pls. 5 and 6) illustrated one of the teeth of *Ziphius sowerbiensis.* He showed six or seven layers of dentin and cementum, but did not comment on the possibility of their being annual layers.

***Ziphius cavirostris* (Cuvier's beaked whale)**
Kenyon (1961) sectioned teeth of two *Ziphius cavirostris* – a 658 cm-long female having 24 to 28 growth layers and a 544 cm-long male having 13 growth layers. He thought that each layer represented a year's growth.

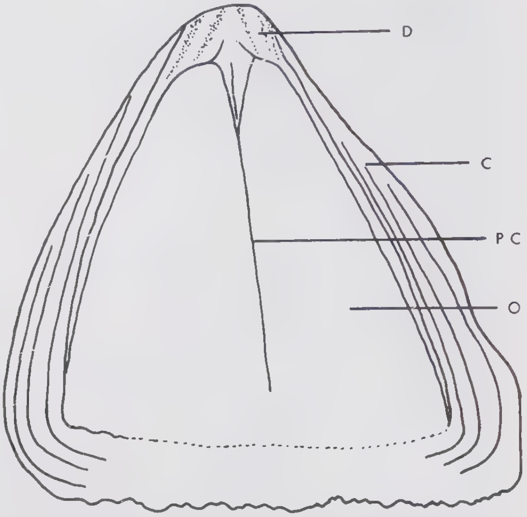

Fig. 3. Diagram of a tooth of a Baird's beaked whale about 4 years old; longitudinal section. D = dentin, C = cementum, PC = pulp canal, OD = "osteodentine". (After Omura *et al.*, 1955, Fig. 26).

***Hyperoodon planifrons* (southern bottlenose whale)**
One of the earliest illustrations of layers in odontocete teeth was presented by Eschricht (1845). There is no indication that he was aware of the significance of the layers.

Cetacea: Delphinidae

***Orcinus orca* (killer whale)**
Sergeant (1959) examined the teeth of a killer whale from eastern Canada. He stated briefly that the growth pattern was similar to that in *Globicephala* and *Tursiops.*

***Globicephala spp.* (pilot whales)**
Sergeant (1959, 1962b) made a detailed study of teeth from at least 694 long-finned pilot whales *(G. melaena)* collected in 1951–59 from Newfoundland. Both dentin and cementum are layered.

> The tooth of a pilot whale is relatively short, and a single cross-section cut in the upper part of the root will pass through all growth layers and enter the pulp cavity. A longitudinal section shows the varying thickness of each growth layer from its apex in the crown to its termination in the root, and the extent of the pulp cavity. [Ten to fifteen layers are deposited before the cavity fills.] However, transverse and longitudinal sections were found to give similar readings of numbers of dentine layers, and the more easily cut transverse sections were employed for routine ageing (1962b, p. 7).

The sequence of zone formation in the dentin is given below. Translucent dentin is said to be poorly calcified. 'This has recently been confirmed by radiography of thin tooth sections' (1962b, p.13).

1st layer. A zone of prenatal dentin followed by a narrow, translucent zone, the neonatal line, which is formed at birth, about mid-August.

2nd layer. An opaque zone passing into a translucent zone, the two representing the nursing period of nearly two years.

3rd and subsequent layers. An opaque zone passing into a translucent zone. Sergeant tentatively assumed that the opaque zone is laid down in August-January and the translucent zone in February-July. The translucent zone coincides with the six-month mating period which peaks in April-May. The largest whales had from 30 to 50 layers.

Although Sergeant had no known-age pilot whales to substantiate his conclusion, he assumed that one layer represents one year. On this basis, the mean age at sexual maturity of females is six years, or the same as the known age at maturity in captive *Tursiops* (interesting, in view of the great difference in size of the two animals; but, see Sacher, this volume).

He also examined the teeth of two short-finned pilot whales, *G. macrorhynchus,* from Florida. The teeth were

> considerably larger than those of *G. melaena* of the same body size. In section they show much thicker dentine, with early deposition of the secondary dentine. . . Growth layers appear to be more frequent than in *G. melaena* of the same length. . . The wide difference in tooth structure between these closely related species is noteworthy (1959, p.285).

Lagenorhynchus acutus (Atlantic white-sided dolphin)
Sergeant (1959) examined the teeth of one white-sided dolphin from the eastern coast of Canada. He found the growth pattern similar to that in *Globicephala* and *Tursiops.*

Delphinus delphis (common dolphin)
Sergeant (1959) examined the teeth of one common dolphin from eastern Canada and found the layered pattern similar to that in *Globicephala* and *Tursiops.*

Kleinenberg and Klevezal' (1962) estimated age in Black Sea common dolphins by comparing the number of dentinal layers in the teeth with the number of bone layers in the lower jaw and the number of corpora albicantia. They examined 33 dolphins taken in July and September 1961. They decalcified entire(?) teeth and cut longitudinal sections. Evidently one layer of bone is laid down each year and 'the number of layers in the dentine of the tooth exactly doubles the number of layers in the lower jaw plus or minus one' (translation, p. 6). Two light and two dark layers are laid down each year in the dentin. The oldest dolphin in the collection was an 11-year male with 11 layers in the jaw bone and 22 zones in the teeth. The authors concluded that most females attain sexual maturity at age two.

Tursiops truncatus (bottlenose dolphin)
Sergeant (1959) was fortunate in obtaining teeth of two bottlenose dolphins of known age, born in the aquarium at Marine Studios, Florida. One was six months old and the other 28½ months. He also obtained the teeth of two old males and one old female, both of unknown age, though held for known periods in the aquarium.

According to Sergeant *(op. cit.)* the growth of the root by increments of cone-shaped dentin resembles that of *Stenella.* The neonatal line, laid down shortly after birth, is clear and unstainable. Following the neonatal line are alternating zones of wide, dense, heavily staining dentin and narrow, clear, poorly staining dentin, repeated at regular and gradually decreasing intervals until the pulp cavity is reached. Two zones, or one layer, are deposited annually.

The daily rate of deposition of dentin as seen in a mid-longitudinal section was estimated to be:

in a known-age male, age 6 months	2.0 microns
in a known-age female, 28½ months	
during the first year only	1.8 microns
during the second year only	1.7 microns
in a male with 8 layers	1.0 microns
in a male with 10 layers	0.8 microns
in a female with 17 ± layers	0.2 microns

The rate of tissue deposition in the female seems to be considerably slower than in the male.

Stenella coeruleoalba (striped dolphin)
Nishiwaki and Yagi (1953) were pioneers in the search for age indices in the teeth of cetaceans. They sought first to learn the rate of deposition of dentin in the teeth of the striped dolphin, a species commonly taken in Japanese waters. In 1951 they injected lead acetate into four captives and released them in Mito Aquarium. The dolphins would not feed; the first one to die survived only five days and the last one fourteen days. From each dolphin they removed the 20th tooth from the posterior end of the jaw in each quadrant (our Fig. 4). They sectioned the teeth transversely

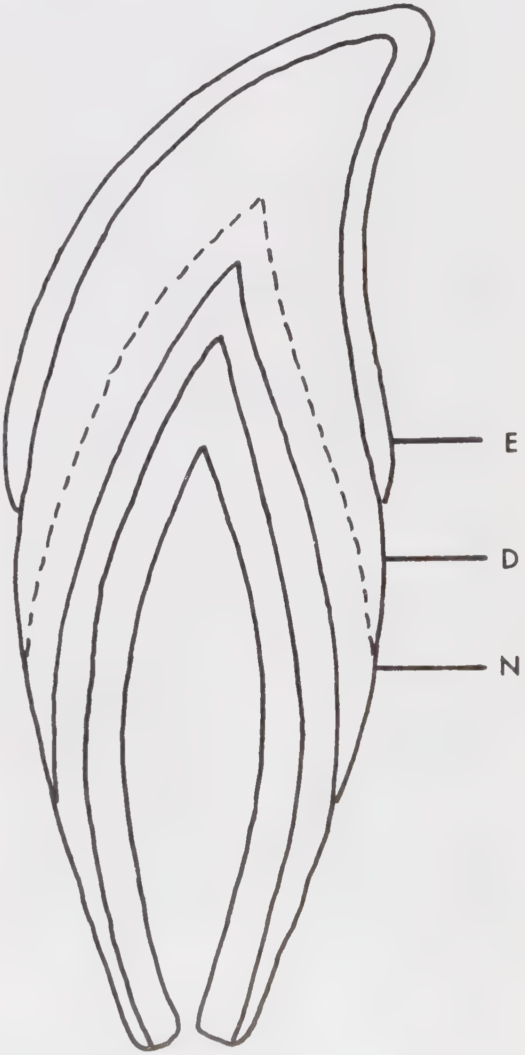

Fig. 4. Diagram of a tooth of a striped dolphin (*Stenella coeruleoalba*) 3 years old; longitudinal section. E = enamel, D = dentin, N = neonatal line (After Nishiwaki and Yagi, 1953, Fig. 3).

or longitudinally. A distinct lead line was visible in the teeth of two animals that lived seven and fourteen days.

Later, the authors examined teeth from 35 males, 55 females, and 16 fetuses collected in 1951. They concluded that the typical zones in a longitudinal section of the root of a large tooth are, in order of deposition: homogeneous fetal dentin; a neonatal line, poorly calcified and unstainable with hematoxylin; and 'striped' dentin with two to eight stripes, immediately external to the pulp cavity.

On the basis of their 1951 sample, plus 98 sets of teeth collected in December 1951 and in 1952, the authors explored further the relationship between dentinal layers and age (Nishiwaki and Yagi, 1954). The number of layers showed a close relationship to body length. The logarithm of the number of dentinal layers showed a positive linear relationship to body length; the shortest individuals had one layer and the longest individuals had eighteen layers. Well-stained zones are deposited in, or shortly before, December and again in May-June. 'Thus it seems by these facts that the deep stainable layer might be made twice a year, but we cannot say at present anything with certainty' (p. 403).

***Phocoena phocoena* (harbour porpoise)**

Sergeant (1959) examined the teeth of two harbour porpoises from eastern Canada. The growth pattern resembles that in *Globicephala* and *Tursiops*.

> In addition . . . the spade-shaped crown, typical of the group [subfamily Phocoeninae], is composed of thick, prenatal dentine and of enamel (p.285).

Pinnipedia: Otariidae

***Allodesmus kelloggi* (an extinct sea lion)**

Mitchell (1966, p. 21) counted 'more than thirteen pairs of light and dark zones' in sectioned teeth of adult male sea lions from the Temblor Formation, late middle Miocene, He saw ridges on the surface of one postcanine.

***Eumetopias jubatus* (Steller sea lion)**

Fiscus (1961) examined the right upper canines of 59 Steller sea lions taken in Alaska in 1958 and found up to 19 growth layers in males and 22 in females. He prepared longitudinal sections by the method of Wilke, Niggol and Fiscus (1958, MS).

Thorsteinson and Lensink (1962) studied another collection taken in Alaska in 1959 from 'harem bulls' only. The teeth were examined by Lensink and Fiscus; 'disagreements . . . occurred in 46% of the sample, but most involved differences of one year and were readily reconciled' (p. 356). The population had a mean age of 10.8 years (6 to > 17).

Spalding (1964) counted layers in the cementum in thin longitudinal sections of upper canines of 138 female sea lions. The first dark cemental zone is deposited in August and September in an animal about 15 months old. It is followed by a light zone, then a dark zone in late summer or fall of the second and succeeding years. He had only one known-age specimen, 16 months old.

***Zalophus californianus* (California sea lion)**

Scheffer (1950, p. 2) saw 'dubious' external growth ridges on the teeth of the California sea lion. Orr *et al* (1970) counted from one to fifteen annual zones on longitudinal sections of upper canines of 35 male sea lions from the Gulf of California.

***Otaria flavescens* (southern sea lion)**

Laws (1962) described growth layers in teeth of the southern sea lion on the basis of several canines collected in the Falkland Islands in late summer. He used longitudinal thin sections, some decalcified and stained. In his Figure 5, the zone pattern looks like a cross section of an old oak stump with numerous fine, regular layers. He suggested the possibility of lunar periodicity in feeding, with two dark and two light zones deposited each month. He measured the thickness of individual deposits and sketched a theoretical time schedule. The peak of deposition was in July (mid-winter) and the depression was in September-October, the breeding season.

***Callorhinus ursinus* (northern fur seal)**

In 1948, Scheffer (1950) examined teeth of known-age, tagged northern fur seals and found external ridges encircling the root, each ridge representing the accelerated growth of one winter-spring season. In 1950, biologists of the Pribilof seal industry standardized a technique for counting external ridges on the right upper canine tooth. They estimated age to ten years and pooled older ages as 'ten-plus'. The age composition of a fur seal population was first published by Wilke (1952, Table 2), for 451 seals taken in waters off Japan.

Wilke *et al* (1958, unpubl.) developed a better technique. They sliced each tooth longitudinally with a bandsaw, ground and polished the flat face, and counted zones in reflected light.

Kubota *et al* (1961, 1963) described development of growth zones on the upper canines (our Figs 5 and 6), as follows:

1. At birth (e.g. in July) the root may not be visible beyond the enamel. The prenatal dentin, all or most of it within the crown, is light colored, the first postnatal dentin is darker; the light and dark zones meet at the 'neonatal line' (which is often not visible).
2. (In summer and fall the root grows slowly.) 'Interglobular spaces' appear in the peripheral dentin, i.e. the region away from the pulp.
3. (The growth rate accelerates in spring.) About the end of April in the life of the pelagic yearling a narrow 'transparent zone' begins to form in the dentin. It terminates on the surface of the root, at the crest of the ridge which marks the end of the seal's first year (in June or July).

Scheffer measured the apical growth on 25 known-age 3-year-old females taken at sea between 23 January and 3 October. He concluded that the ridge does not start to round off, and the summer-fall valley does not start to form, until June. The first indication of a thin shelf representing the beginning of the next ridge is formed in August.

Yagi *et al* (1963) administered lead acetate and tetracycline to a 4-year female fur seal in an aquarium. The seal lived 162 days after the first injection. Both drugs left traces in the dentin which were demonstrable by histochemical methods.

Scheffer and Kraus (1964) studied the morphology and development of seal teeth. Among their conclusions are the following:

1. Dentin gradually fills the root canal until, at ages varying from 3 months (for small incisors) to more than 20 years (for the large upper canines of the male), the root is completely closed.

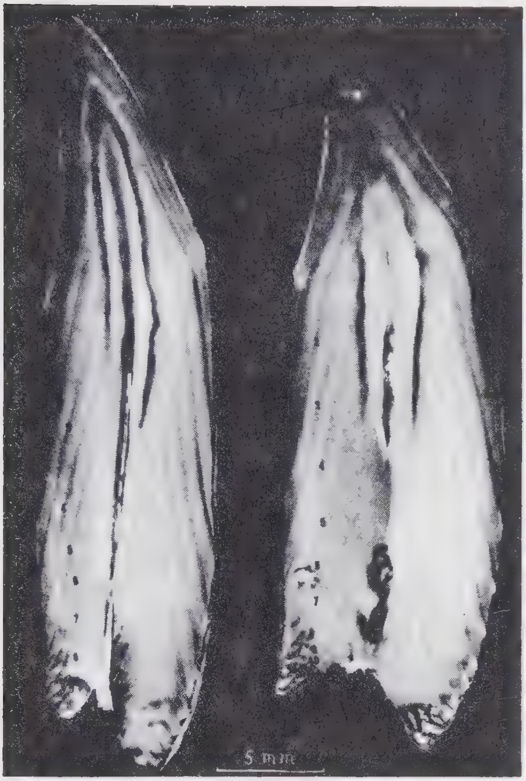

Fig. 5. Upper canine teeth of two female northern fur seals: (left) age 11, taken in mid-August; (right) age 12, taken in mid-July; longitudinal thin sections by reflected light. Numbers indicate the (translucent) dentin deposited in spring. (From Kubota *et al.*, 1963, pl. 1.)

(2) Growth layers in the upper canine of a seal held in captivity from age 3 months to 58 months were abnormal, though could be grouped into five annual series.

(3) 'Ridges on the surface of the growing root, finer than [yearly] annuli and spaced between them, are thought to originate in individual periods of intensive feeding' (p. 309).

Scheffer and Peterson (1967) continued the study of fine ridges. During the 16-week suckling period, about ten or eleven zones are laid down in the dentin of the pup, each representing one period of suckling followed by a fast. The zones are permanent.

Arctocephalus australis **(South American fur seal)**

Mansfield (1958a, p. 39) saw concentric rings in cross sections and surface ridges on canine teeth of ten South American fur seals.

> In the older specimens in which the pulp cavity was almost occluded, a . . . pattern of alternate light and dark rings of dentine was found. As in the Weddell seal a pair of these rings was assumed to represent one year of the life cycle, and the specimens were aged on this basis, the age . . . was found to agree within a year with the age determined by the number of external ridges on the teeth. These ridges are well marked, and the teeth resemble those of the Alaskan fur seal for which the method has been proven valid.

The source of the ten specimens was not given, though Mansfield wrote (in letter of 17 February 1967) that 'they most probably came from J.E. Hamilton's Falkland Islands fur seal collection in the British Museum.'

Arctocephalus pusillus **(Cape fur seal)**

Rand (1956, p. 12) found that in teeth of the Cape fur seal 'the numerous annuli showed no discontinuous pattern that

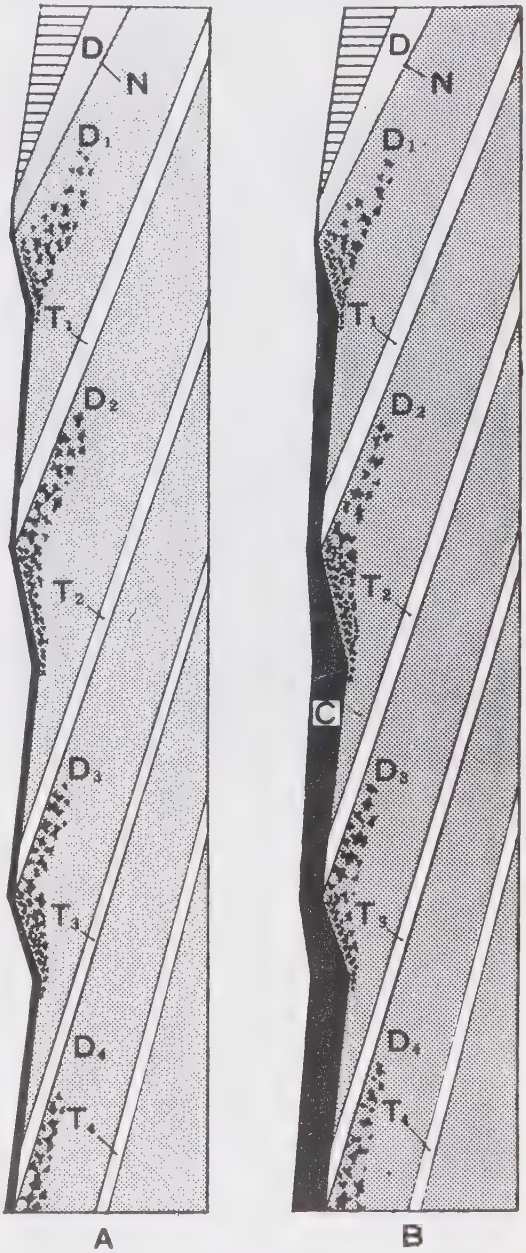

Fig. 6. Diagram of upper canine teeth of northern fur seals, (A) "young" and (B) "old"; longitudinal thin sections by transmitted light. C = cementum, D = prenatal dentin, N = neonatal line, D 1 to 4 = opaque dentin deposited in 1st to 4th years; T 1 to 4 = "transparent" [translucent] dentin deposited in 1st to 4th years. (From Kubota *et al.*, 1961, pl. 7.)

could be correlated with definite annual or other recognizable time units.'

Pinnipedia: Odobenidae

Odobenus rosmarus **(walrus)**
It has long been known that ridges surround the root of the tusk in some old walruses, particularly old males (our Fig. 7). The ridges are partly obscured by cementum but are revealed when the cementum is chipped away or when the tusk is sectioned lengthwise. Cemental layers are also deposited on the premolars.

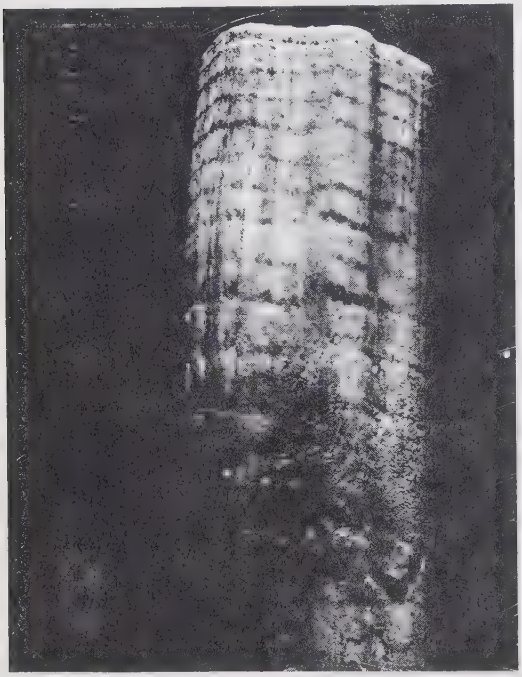

Fig. 7. Tusk of an old male Pacific walrus showing annual ridges. Date of death unknown, a subfossil from beach sands of St. Paul Island, Alaska. A very large tusk, total length along convex surface 917 mm (36.1 inches). (VBS photo 2509A.)

The pioneer work of Chapskii (1941) on walrus teeth has been mentioned. Mohr (1943, p. 259) stated that

> longitudinal and transverse sections through the teeth of walruses of known age reveal that the cemental hyperplasia takes place in the form of yearly rings, similar to the otoliths and bones of fish.

In 1952, Brooks and Fay independently undertook studies of the Pacific walrus *(O.r. divergens)* (Brooks, 1954, unpubl.; Fay, 1952, unpubl.). They focused on interpretation of the cemental layers of the premolars. Brooks concluded that one dark ring or none is deposited in the first year and two dark rings (summer and winter) in each year of life after the first. He correlated estimated age with number of cementum rings on the premolars and with tusk length. In his Figure 9, for example, he indicated that an 8-year-male with tusks one to fifteen inches long has fifteen rings.

Fay (1956, unpubl.) described criteria for each year class from newborn to age four, using length of tusk, wear of enamel on the tusk, degree of staining of the teeth, cranial and body size, observation of the adult female (presumptive mother) with the young animal, and reproductive history of the mother as revealed by autopsy. Available to him were teeth from seven Pacific walruses and nine Atlantic walruses of known age, raised in zoos. He counted the cemental layers on sections of the second upper premolar or the first lower premolar. In the Pacific walrus, two or three zones of cementum are deposited the first year, decreasing to one layer per year at time of sexual maturity. In the Atlantic walrus *(O.r. rosmarus)*, one or two layers are deposited before sexual maturity and one thereafter. In very old Pacific walruses, as many as four initial layers of cementum have disappeared through wear.

Longitudinal sections of the tusk of the Pacific walrus show up to 30 marginal ridges and indicate an age of 30-plus years. In specimens collected in May, the ridge is at the apex of the root. In specimens taken in the ensuing twelve months the zone between the ridge and the apex of the root widens progressively at a rate such that by the next May the ridge is again at the apex. Thus, the ridge is clearly an annual mark. Although the ridge count may be indicative of minimum age in years, the cemental layer count in the premolar roots is more consistent.

In the spring and summer of 1960, Samuel J. Harbo began a study of walrus in the Bering Strait and vicinity (Harbo, 1961). He collected the teeth, mainly lower canines, of 886 walruses. He standardized a method of sectioning the teeth longitudinally and of counting zones in cementum. He used the formula: two zones per year through the fifth year and one zone per year in the sixth and subsequent years; plus a factor varying from one to three years to correct for loss through attrition. He concluded that the oldest males and females were 28 and 26 years old, respectively, but according to Burns (1966, p. 5)

> . . . closure of the root apex most commonly occurs between the fifth and sixth years of life . . . it is probably not possible to determine the age of very old individuals.

Mansfield (1958b) studied 176 walruses from the northwestern Atlantic. He was able to classify calves, yearlings, and 2-year-olds, but not older animals, by body and tusk measurements. With regard to cemental layers on the premolars of the male, he stated:

> It is assumed that after the second year, one well defined layer of cementum is laid down annually, and this continues throughout the life of the animal (p.39).

He was confident that he could age males, but not all females, from counts of cementum layers on the premolars.

Pinnipedia: Phocidae

Phoca vitulina **(harbour seal)**
Mansfield and Fisher (1960) examined an upper canine tooth of an old male harbour seal which had been held in captivity from its first summer. In thin cross sections they counted 18 to 20 cemental layers. They learned later that the seal was 19½ years old.

> There were no clearly marked dentinal layers . . . but examination of other canines from both male and female harbour seals has shown that, where dentinal layers are present, they agree in number with those in the cementum (p. 93).

Each cemental layer contains a wide opaque zone and a narrow translucent zone. The narrow zone is

> laid down in the spring and early summer and may represent a period of minimal feeding during the breeding period and the moult (p. 93).

In 1969, Michael Bigg completed a study of harbour seals from British Columbia. He wrote (1969, p. 8) that translucent layers are laid down in the cementum between late autumn and late spring, and opaque layers between late spring and late autumn.

Phoca hispida **(ringed seal)**
McLaren (1958a) made cross sections of teeth from more than 750 ringed seals and estimated age from counts of dentin layers. The oldest seal, a male, had more than 43 layers. He validated his method by counting bands on the claws. Sections of the teeth show the following sequence:

> *Mid-July to mid-March of the following year* – translucent dentin is deposited.
>
> *Mid-March to mid-July* – opaque dentin is deposited. It becomes increasingly reflective and vacuolar in June and early July when the seals are fasting, basking on the ice, and molting.

Tikhomirov and Klevezal′ (1964, Fig. 1) published a photograph of a cross section of a ringed seal tooth, as did Klevezal′ (1964, Fig. 1).

Phoca groenlandica **(harp seal)**
Fisher (1952) was first to estimate ages of harp seals by growth layers in the teeth. The oldest in a sample of 375 seals was about 28 years old. Fisher and Sergeant (1954, p.1) stated that

> because the reading of annual rings is not always exact, the totals for the ages of nine years and up are smoothed [on a graph] by fives.

And Sergeant and Fisher (1960, p. 36) noted that

> the relative strength of a year class can be detected [through tooth reading] up to five or six years; after this age, errors in age determination . . . obscure the real fluctuations in year-class strength.

According to Fisher (1954) the zones of dentin are laid down as follows. The *translucent* zone is laid down in November-March during the period of active feeding on the southbound migration and during the breeding season. The *opaque* zone starts to form during the molt (April-May) and continues to form during the northward migration and summer wandering in the Arctic (June-September).

Rasmussen (1957) published a photograph of a thin cross section of a 7-year-old harp seal tooth. He described the formation of 'white' zones laid down in feeding periods, mainly during summer, and 'dark hyaline' zones laid down in fasting periods such as molting and breeding periods in early spring.

> As the animal becomes older, the pulp cavity becomes filled with dentine, and in old animals the cavity is completely closed. This sets a limit on how far we can trace the age of an animal. With reasonable accuracy, we can read ages of 15 to 17 years, but we have specimens showing clear readings up to 27 years (p.52).

Phoca fasciata **(ribbon seal)**
Tikhomirov and Klevezal′ (1964, Figs. 2 and 5) illustrated cross sections of ribbon seal teeth. They counted cemental layers but concluded (p. 19) that age determination from claws is easier and more practical, because these do not wear appreciably with age.

Klevezal′ (1964) was interested in determining the age of sexual maturity in the ribbon seal. From counts of dentinal layers in cross sections of canines she showed that maturity in both sexes is reached by the end of the third or fourth year.

Erignathus barbatus **(bearded seal)**
Allen (1880, pp. 654–655) described the dentition of the bearded seal as

> teeth small, molars spaced, slightly implanted, early becoming defective by attrition; partly deciduous in old age, . . . Quite early in life the teeth become much worn, and in old age the crowns of the three middle molars become often wholly worn away, leaving only the fangs [roots], and even these sometimes in part disappear.

McLaren (1958b) concluded that he could not determine age from the teeth but that growth increments in claws were useful as age indicators.

Tikhomirov and Klevezal′ (1964, p. 19) concluded that bone strata in the lower jaw are the best indication of age.

Cystophora cristata **(hooded seal)**
Rasmussen (1957) made the first systematic collection of hooded seal teeth in Denmark Strait in 1954. (Sealing crews had saved the lower jaws.) A male pup in the natal 'blueback' pelage was tagged in 1951 and recaptured at age five as a 'bladdernose' in 1956. Presumably its teeth were used to calibrate the age-reading method. In a sample of at least 25 males and 22 females, the oldest male was 25 years old and the oldest female 24 years.

In his report on a sample of some 6,000 hooded seals, Rasmussen (1960) provided the following description of the canines:

> In the tooth's dentine we find alternating dark and light bands. As the seal gets older, layer after layer of white dentine is laid down round the pulp canal divided by dark layers. The pulp canal is eventually filled with dentine and in very old animals the central part will be almost completely closed. In hoods [sic] a thick layer of cement is also laid down annually on the tooth's outer surface. This layer may become very thick, especially in older animals. In this outer layer we can find closely spaced rings which in numbers agree with those we find inside the tooth itself. By counting both the inner and outer rings one can get a good check on the accuracy of age determination, especially in older animals (1960, p. 14, in translation).

A study by Øritsland of the breeding of the female hooded seal was based principally on examination of ovaries from 371 animals, all aged by dentin layers in the canine teeth (Øritsland, 1964, p. 14). The seals were collected in waters of Jan Mayen and Denmark Strait. Thirteen (or 3.5%) were described as age '21+'.

'Hansi', an adult male hooded seal, died in Tiergarten Bremerhaven in 1954 after 14 months in captivity (Mohr, 1966). Mohr photographed a thin cross section of one of Hansi's lower canines and estimated his age at 14 to 15 years. The photograph shows a very wide series of cemental layers (our Fig. 8).

Halichoerus grypus **(gray seal)**
Hewer (1960, 1964) examined teeth, mostly lower canines, of 295 gray seals. He had known-age specimens from classes 0 to 1 year, 6 years, 12 years, and 27 years. Since the pulp canal closes in the fifth or sixth year, he counted both dentinal and cemental layers up to about the fifth year, then cemental layers only (our Fig. 9).

Deposition of cementum in the gray seal is complex. Cementum first appears on the root of the lower canine

> about three to four months after birth, somewhat unevenly in two bands on the root. Afterwards, these bands coalesce (*op. cit.*, 1960, p. 960).

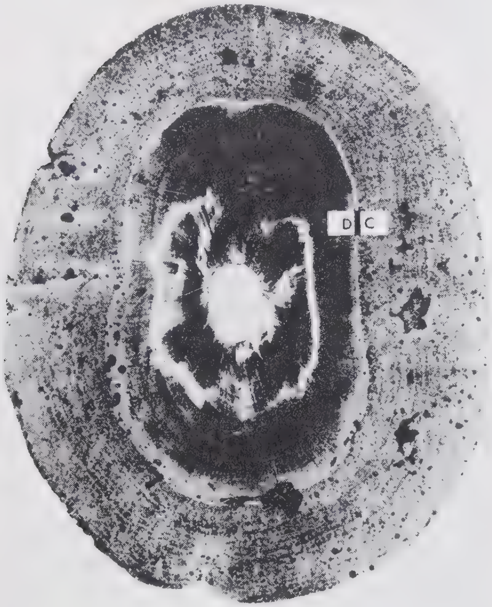

Fig. 8. Lower canine of a hooded seal, male 14–15 years old; thin cross section. DC = junction of dentin with the very thick cementum. (After Mohr, 1966, Fig. 2.)

For estimation purposes, October is assumed to be the mean month of birth; thus the first cementum appears in January or February.

The next layer of cementum is accumulated in September when the seal completes its first year of growth. All annual layers can be identified by the more translucent appearance toward the outer (alveolar) edge. In the second year, cementum spreads rapidly over the apex of the root, stopping all further growth of the dentin toward the apex, but deposition of dentin continues as a series of decreasingly smaller cones for another four or five years.

Monachus schauinslandi **(Hawaiian monk seal)**

Kenyon and Fiscus (1963) examined the right upper canines of two adult Hawaiian monk seals, a male estimated at 20 years old and a female at 11. There were no surface ridges; the pulp canals were closed; on longitudinal sections the dentin showed [annual] layers and layered cementum. The cementum on the male tooth was up to 7 mm thick and on the female tooth up to 3 mm. The layers of cementum did not decrease in thickness with advancing age.

The monk seal does not migrate.

> It may be concluded that . . . fasting, probably during molt, causes visible annular [i.e. annual] interruptions in the deposition of cementum and dentin which may be used as an indication of age . . . The pulp canal of the canines appeared to have filled completely at four or five years as indicated by visible layers in the dentin (p. 281).

Mirounga leonina **(southern elephant seal)**

Laws proposed a new method of age determination for

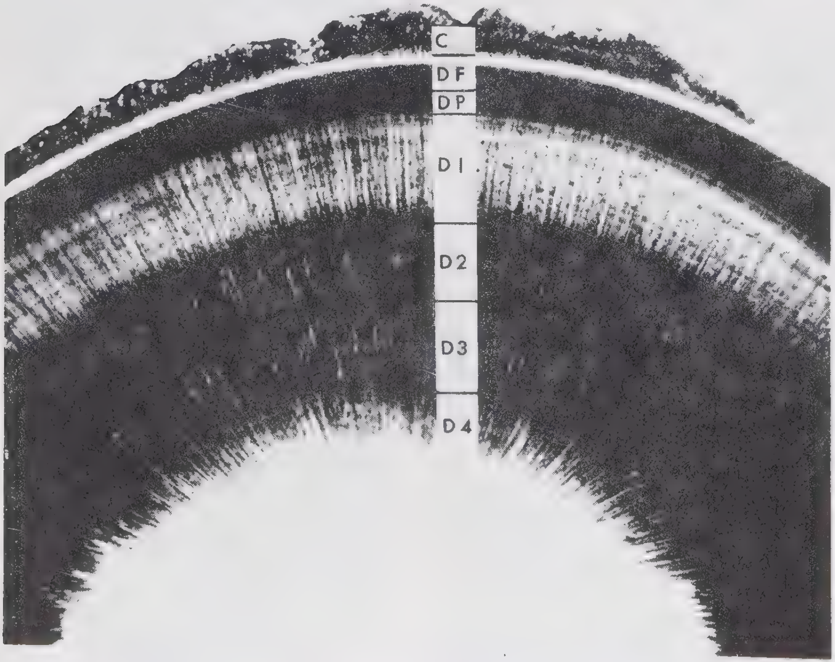

Fig. 9. Lower canine tooth of a gray seal, age 3 years, 8 months; thin cross section by transmitted light. C = cementum (separated from dentin by a clear artifact), DF = fetal dentin, DP = pup dentin, D 1 to 4 = dentin of 1st to 4th years. (After Hewer, 1964, pl. 1, Fig. 3.)

mammals largely from studies of elephant seals at the South Orkneys (1952, 1953a). He continued to study elephant seal teeth, with a special interest in microstructure and its metabolic implications (1953b, 1959, 1960, 1962).

> The canine teeth . . . grow continuously throughout life; the pulp cavity remains open and attrition is negligible (1953a, p. 3).

At the level of the alveolar aperture all annual layers are exposed.

The permanent canines erupt at an average age of eight days (lower) and ten days (upper). Inside the fetal dentin, a sharp neonatal line serves as a starting mark for counting annual layers. It is followed by a variable series of zones laid down through adolescence to sexual maturity. Maturity may occur at the end of the third year in males and the second year in females. In the fourth and later years, four zones a year are laid down rather consistently in both sexes. These include two zones of translucent dentin ('columnar') alternating with two zones of opaque ('marbled').

Although Laws did not have known-age seals older than pups, he proved indirectly that the four-zone group must represent one year's increment (1953a, p. 6). The first recaptures of known-age elephant seals, 18 branded individuals, were reported by Carrick and Ingham (1960, p. 329).

Laws (1953a, p.4; 1960, p.10) suggested the following development of hard and soft layers of dentin:

(1) a hard zone is deposited in the spring breeding period (mid-September to mid-November);
(2) a soft zone is deposited in the early summer feeding period (November and December);
(3) a hard zone is deposited in the late summer and autumn molting period (January to early May); and
(4) a soft zone is deposited in the winter feeding period (mid-May to mid-September).

Carrick and Ingham (1962) gave a detailed description, with 69 photographs and 2 diagrams, of canine tooth structure in the elephant seal. They used known-age animals, 20 males and 17 females branded as pups on Macquarie Island in 1951–59 and killed in 1956, 1957, 1959, and 1960. The oldest was 8 years, 3 months old. All four canines were saved and were treated by various methods designed to reveal dentinal layers to best advantage without the labor of cutting thin sections (our Fig. 10).

The findings of Carrick and Ingham differed from those of Laws for certain reasons:

(1) at South Georgia, where Laws worked, the male and female seals mature sexually at two and four years, respectively (Laws, 1960, p. 472; at Macquarie they mature at three to five and six years, respectively.
(2) Carrick and Ingham had the advantage of known-age specimens, many of them representing the younger ages. Furthermore, some of the marked animals had been seen and identified in the wild before death, and had been reported as 'ashore in May', 'pre-molt in February', or otherwise.
(3) Carrick and Ingham sectioned the teeth at the top of the pulp cavity where the zones are widest, and they stained the sections; both procedures contributed to a clearer picture of the zones. Carrick and Ingham concluded that 'the pattern of calcification is less simple than Laws suggests' (1962, p.111).

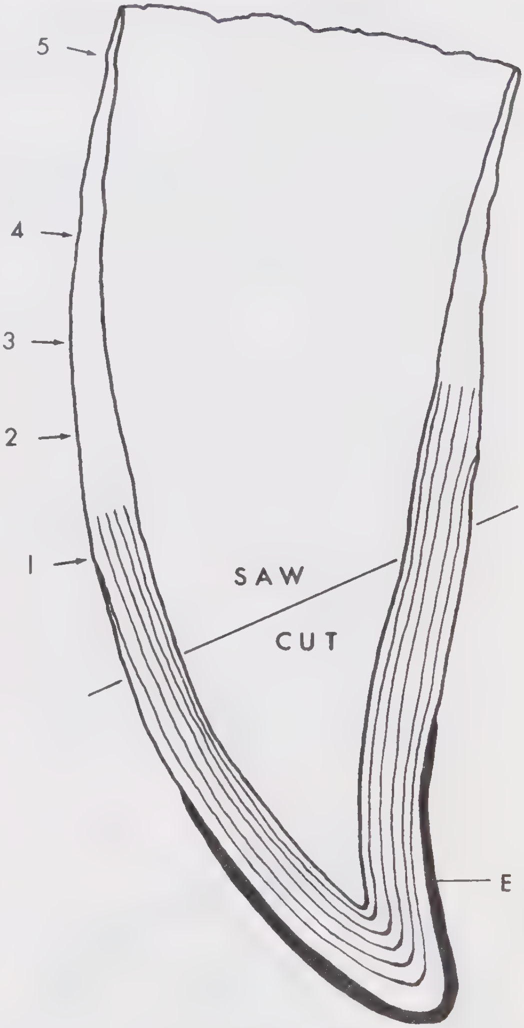

Fig. 10. Lower canine of an elephant seal showing where a typical saw cut is made at the level of the gum to obtain the crown and a portion of the root containing all annual layers. Longitudinal section, diagrammatic; 67-month ("6-year") male. E = enamel; arrows show approximate position of apex at birthdays 1 to 5. (After Carrick and Ingham, 1962, pl. 4.)

Lobodon carcinophagus **(crabeater seal)**

Laws, (1953a, Fig. 4) illustrated a cross section of a lower canine of a male crabeater seal estimated to be six years old. Later, he estimated the ages of 76 crabeaters, some found dead after an epizootic. The oldest were 19 years old (Laws and Taylor, 1957). Laws studied the same sample again (1958) in greater detail. The sequence of zone formation is approximately as follows:

(1) Thick fetal dentin laid down in the first six weeks of pregnancy.
(2) A sharp neonatal ring, about September.
(3) A (presumed) weaning ring five or six weeks later.
(4) A series of fine, irregular, post-weaning layers becoming vacuolated toward the end of the first year, in September or October (spring). The vacuolated zone is white or gray by reflected light and is the most useful zone for indicating age, for it appears each year in spring.

***Ommatophoca rossii* (Ross seal)**
Laws (1953a, p. 9) saw concentric rings on cross sections of a Ross seal tooth.

***Hydrurga leptonyx* (leopard seal)**
Laws (1952) saw concentric rings on cross sections of leopard seal teeth and subsequently (1953a, Fig. 4b) illustrated a section from a canine of a 6-year-old female.

Paulian (1955) counted 'stries d'accroissement' on teeth of six leopard seals from Kerguelen Islands. He felt certain of the ages of three males, one, two, and three years old, but less certain of the ages of three other seals about five to eight years old.

Laws (1957) estimated the ages of 39 leopard seals; the oldest was a male of 16-plus years.

***Leptonychotes weddelli* (Weddell seal)**
Laws (1952, 1953a) saw concentric rings on cross sections of teeth of the Weddell seal.

Mansfield (1958a) examined the teeth of six male and twelve female Weddell seals from the South Orkneys (our Fig. 11). He estimated the age of the oldest male at 16 years; of the oldest female at 14 years. From outside in, by reflected light, the sections show:

(1) wide, dark zone (translucent) dentin deposited in fetal and suckling life;
(2) a wide, light zone of opaque dentin assumed to represent the winter period of feeding at sea;
(3) another translucent zone, now called 'columnar' dentin, assumed to represent the summer period of breeding and molting, with irregular feeding;
(4) another opaque zone, and so on.

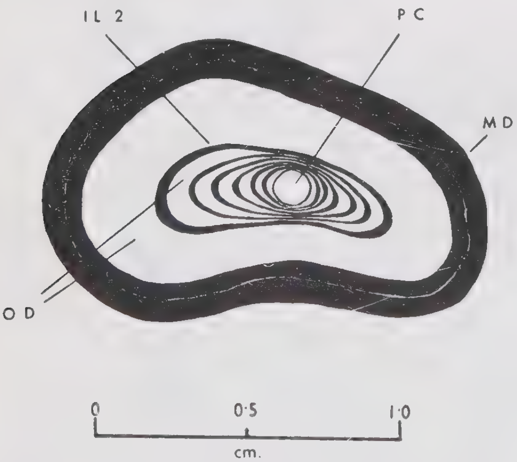

Fig. 11. Diagrammatic cross section of a canine tooth of a female Weddell seal about 8 years old, by reflected light. PC = pulp cavity, MD = "mantle" or translucent dentin presumably laid down up to the end of lactation, OD = opaque dentin, IL 2 = inner limit of 2nd year's growth. (After Mansfield, 1958a, Fig. 17.)

Sirenia: Dugongidae

***Dugong dugon* (dugong)**
Pocock (1940) used body length and cranial sutures as criteria of physiological age in dugongs. Scheffer (1970) studied dentinal layering in the tusk, using etched, half-tooth and longitudinal thin sections. Dentin seems to be deposited with annual, monthly, and perhaps even daily periodicity.

CONCLUSION

Research interest in the layering of marine mammal teeth began to quicken about thirty years ago. Now the tooth layers of thousands of individuals are routinely read each year as a procedure in life-history analysis. Despite their wide use as age indicators, tooth layers remain poorly understood with respect to their etiology, biochemistry, and physiology. The problems of preparing teeth for examination and examining and interpreting teeth layers will be dealt with in the papers which follow.

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INTRODUCTION OF TRIPARTITE AND SEA GRANT RESEARCH PROGRAMS IN THE NORTHWESTERN HAWAIIAN ISLANDS

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Mr. Chairman, distinguished guests, Northwestern Hawaiian Islands (NWHI) symposium participants, ladies and gentlemen. I am indeed honored to be invited to make a few introductory remarks to open this symposium.

I am sure all of you are aware that the NWHI study is still an ongoing and active program and that this symposium is primarily a mechanism to evaluate and assess the results achieved to date. We need this midstream pause to avoid the triple-S disease--Shomura's should've syndrome--a disease which is characterized by a feeling, after the fact, that we should've done this, or should've done that.

Before providing you with some background information on the rationale for the NWHI investigation, I would like to briefly describe the NWHI and state the general objectives of this study.

First, to clear up some nomenclatural problems, the string of islands under investigation is commonly known as the Leeward Islands. Since Leeward is such a nondescript term and could refer to one of several leeward islands located throughout the world, I prefer to follow the State of Hawaii's lead and refer to this part of the Hawaiian Archipelago as the NWHI.

The NWHI are made up of a group of low, rocky islets and coral atolls extending more than 1,000 miles in a northwesterly direction from Nihoa Island to Kure Atoll. Geologically, the NWHI are markedly different from the main Hawaiian Islands. The main islands on which we live are of recent geological vintage, volcanic in origin, and are characterized by high mountains and relatively large land masses. These large land masses--the main islands--even before discovery by man, contained a wide variety of plants and animals. In contrast, the NWHI include a relatively impoverished land fauna, in a limited terrestrial habitat.

Today, many people would describe much of the NWHI area as pristine. Historically, this was not the case. In the late 1800s entrepreneurs began mining operations for guano at Laysan and Lisianski Islands. The non-pristine situation was aptly described in an article which appeared recently in a local newspaper. Besides giving an account of the primitive living conditions on Laysan, there is a description of the havoc caused by the introduction of rabbits on Laysan Island. In addition to mining, others set up harvesting bases to collect feathers of seabirds. In the late 1920s pearl shells were harvested from the lagoons of Pearl and Hermes Reef.

To protect the birds of the NWHI, President Theodore Roosevelt in 1909 designated the area as "The Hawaiian Islands Bird Reservation." In 1940 the area was redesignated "The Hawaiian Islands National Wildlife Refuge" and in 1966 the refuge became a part of "The National Wildlife Refuge System." The State in 1952 also designated the area as a State wildlife refuge.

The NWHI are part of an interesting maze of ownership and jurisdiction. All of the islands from the Big Island to Kure are part of the Hawaiian Archipelago. With the exception of Midway all of the islands are considered part of the State of Hawaii. With the exception of Midway and Kure all of the islands of the NWHI are a part of the Hawaiian Islands National Wildlife Refuge. While the NWHI can be considered legally part of the State of Hawaii, the actual administration of the islands rests with the Fish and Wildlife Service since all except Kure and Midway come under the Wildlife Refuge System. For the management of fish and wildlife on Kure, I believe the State has adopted a policy that is essentially in consonance with Federal regulations.

The NWHI are a classical example of the problems mankind presently faces in allocating access to and availability of resources. Decisions on allocation inevitably must be made in the general framework of "what's best for the nation." Since mankind in this case primarily refers to the citizens of Hawaii and the rest of the nation, we will need to identify the players.

Who are the players with interest in the NWHI? First, there is the naval force on Midway. The Navy command on Midway fluctuates in size depending upon the world military situation, but they generally keep a low profile. The Coast Guard is currently on Kure Island maintaining a loran station. Until last year the Coast Guard also occupied French Frigate Shoals where they maintained a loran station. This station was phased out in 1979. The third group includes the commercial and recreational fishing interests. It should be pointed out that commercial fishing in the NWHI took place before the World War II years. Much of the fishing activity, however, was confined to the lower sectors of the NWHI. Then there is also the interest in the NWHI of the scientific community. The first scientific study of the NWHI was undertaken by the U.S. Fish Commission in 1902 on the research vessel Albatross. Since 1902 research in the NWHI has been sporadic. After nearly three decades of little or no scientific activity in the area, Paul Galtsoff, a fishery biologist in the old U.S. Bureau of Fisheries, undertook an investigation of Pearl and Hermes Reef in 1930. Finally, among the cast of players is a segment of society which has a deep interest in conserving and preserving the fauna and flora of the NWHI.

What are the resources of interest to these special interest groups? First, the military is simply interested in Midway Islands as an operational base, although at one time they were deeply interested in the avifauna. Their interest in the avifauna was primarily in trying to eliminate albatross or at least to discourage the nesting of albatross on the aircraft runway. The fish and invertebrate resources of the NWHI are of interest to the commercial and recreational fishing community. These resources are not completely understood in terms of availability and abundance.

There are many species of seabirds that live and nest in the NWHI. There are also several endemic land birds associated with these islands. These include the Laysan duck, Laysan finch, Nihoa finch, and the Nihoa millerbird. Among the seabirds are the familiar Laysan albatross, black-footed albatross, frigatebird, noddy tern, boobies, shearwaters, and a handful of other species.

For marine mammals, the NWHI is home for the endemic Hawaiian monk seal. The Hawaiian monk seal is presently on the endangered species list, since there is some evidence that the population is declining. Because the number making up the total population of seals is in the order of hundreds and certainly less than several thousands, there is cause for concern. Finally, there is the green sea turtle which nests in the NWHI and is currently on the threatened species list.

All of my ramblings to this point leads up to the general objective of why we are studying the NWHI. Even if society in general was not interested in the area, the isolated nature of the Hawaiian Archipelago and the fact that it is in the outer reaches of the Indo-Pacific fauna would in itself be of tremendous scientific interest and inquiry. The fact that various segments of society have expressed interest in the area, some with conflicting views, makes our investigation even more crucial and necessary. I would like to think that our overall objective is to gain knowledge and understanding of the NWHI marine ecosystem to provide decisionmakers with a sound basis for the utilization or non-utilization of the resources of the area.

I've often wondered what will happen to the NWHI if and when the ice caps melt as has been predicted. If the melting ice caps were to appreciably raise the sea level in the NWHI will the Hawaiian monk seal, if not extinct by then, adapt to a rocky shore habitat? How about the poor green sea turtle that needs to dig her nest in sand; she will find "tough sledding" on rocky shores. Finally, will the albatrosses be able to adapt, possibly ending up nesting on the slopes of Haleakala? Returning to the realities of the present, what we need to know about the resources today is how much is available, and of more importance, the interactions of the various components of the ecosystem. Although we need a quantitative measure of the resources available in the area, it is more important to know what effect the various components of this ecosystem have on each other. What are the pressure points? Is the abundance of the Laysan albatross controlled by availability of food or is it associated with other environmental factors such as temperature?

The process by which we embarked on this study may be of interest to some of you. The Honolulu Laboratory in 1973 went through a major reorganization. In Federal Government circles a major reorganization usually means a cut in budget and a reduction in force. These two things took place in 1973 and the Lab was in a demoralized and chaotic condition. In an early planning session I had with several key staff members we agreed that one way to revitalize the Lab was to embark on a new program, a program that would generate interest, be high on the scale of regional or national needs (this in light of the budget situation) and one which had appeal and could be "sold" through the system. Since we could see the problems that were beginning to surface within the NWHI, it seemed like a study of the NWHI would be important, have high visibility, and would be a program that could generate fiscal support. In the early 1970s preservationists were gathering support to close the NWHI to all human activities; others with commercial inclinations were beginning to be concerned that fishing access to the NWHI would be closed off. The Navy at Midway remained silent and the Coast Guard kept trying to accommodate the many State and Federal regulations and guidelines that control the area.

A quick review of the literature revealed that very little was known of the fauna and flora of the NWHI. It distressed me a bit when I realized that we at the Honolulu Laboratory knew more about the resources of the tropical equatorial Pacific, the pelagic waters of the North Pacific, and even the resources of the Indian Ocean than we did the resources of the NWHI.

In late 1973 we undertook some preliminary field work in the NWHI on the NOAA research vessel David Starr Jordan. Encouraged by our early findings we began a major push through our budgeting cycle to obtain funds to carry out a long-term program. We were successful to a limited extent. We recognized that in the Federal climate of the mid-1970s, obtaining funds and personnel ceilings were difficult. Realizing that the Honolulu Laboratory could not do the entire job properly, I approached the Fish and Wildlife Service, the State Fish and Game, and the University of Hawaii Sea Grant College Program about pooling our collective resources and undertaking a cooperative investigation of the NWHI. I received immediate and positive responses from the Fish and Wildlife Service and Fish and Game. From Sea Grant I received neither a positive nor a negative response. I guess one could say the suggestions of cooperative effort that I made at the Sea Grant advisory meetings fell on deaf ears. In fairness to Sea Grant, the program at that time was embroiled in a tremendous task of reorganizing its aquaculture program. Since that was Sea Grant's largest program at that time it probably took up all of the energy the Sea Grant leadership could then generate.

In any event, I met with Fish and Wildlife Service and Fish and Game officials to scope out a cooperative program. We decided to allocate the research areas pretty much in line with organizational responsibilities; thus, the Fish and Wildlife Service was to undertake research responsibility for the seabirds, Fish and Game for the nearshore fishery resources, and the Honolulu Laboratory for the slope, banks and offshore resources. We found out later that the National Marine Mammal Laboratory of the Northwest and Alaska Fisheries Center, National Marine Fisheries Service in Seattle had research plans for monk seals. In the meantime, we continued to plan cruises to the NWHI from 1975 to 1978. To formalize the cooperative research agreement we developed a document that detailed the plans for the various agencies in a tripartite agreement to conduct research in the NWHI. Although the agreement was signed in 1978, the cooperative research was initiated much earlier. Incidentally, as of mid-1979 the Honolulu Laboratory was given the responsibility for research on Hawaiian monk seals and green sea turtles.

Returning to Sea Grant involvement, or lack of involvement, the best thing that happened to the Sea Grant Program was the return of Dr. Jack Davidson to Hawaii in 1977. An equally fortunate event was the return to the University in late 1977 of Dr. Rick Grigg, who had spent a year in Washington, D.C. Rick was eager to resume his research activities and approached me about some sea time on our research vessel to collect data on precious corals in the NWHI. I took this opportunity to give Rick a long discourse, expressing my disappointment with Sea Grant for its lack of involvement in the tripartite study. As you can probably guess, Rick, with support from Jack Davidson, quickly prepared a NWHI package for Sea Grant support.

As evidenced by its current deep involvement with this symposium, Rick was successful in influencing Sea Grant to become a full partner in the NWHI studies. The studies currently being supported by Sea Grant are complementary to those being carried out by the other three agencies. In their study of primary productivity and the oceanographic environment in the NWHI, Sea Grant is filling a major research gap.

During the presentations today and tomorrow you will be hearing about some extremely interesting and exciting research. I believe some of the results will turn out to be major contributions toward our understanding of tropical reef ecosystems.

In closing, it is my hope that the final product of this cooperative undertaking will be a monograph bearing a title something like "The NWHI--An Ecosystem Successfully Dissected and Analyzed." Furthermore, I would like to see a paperback version of this monograph entitled "Everything you wanted to know about the NWHI but were afraid to ask."

Thank you.

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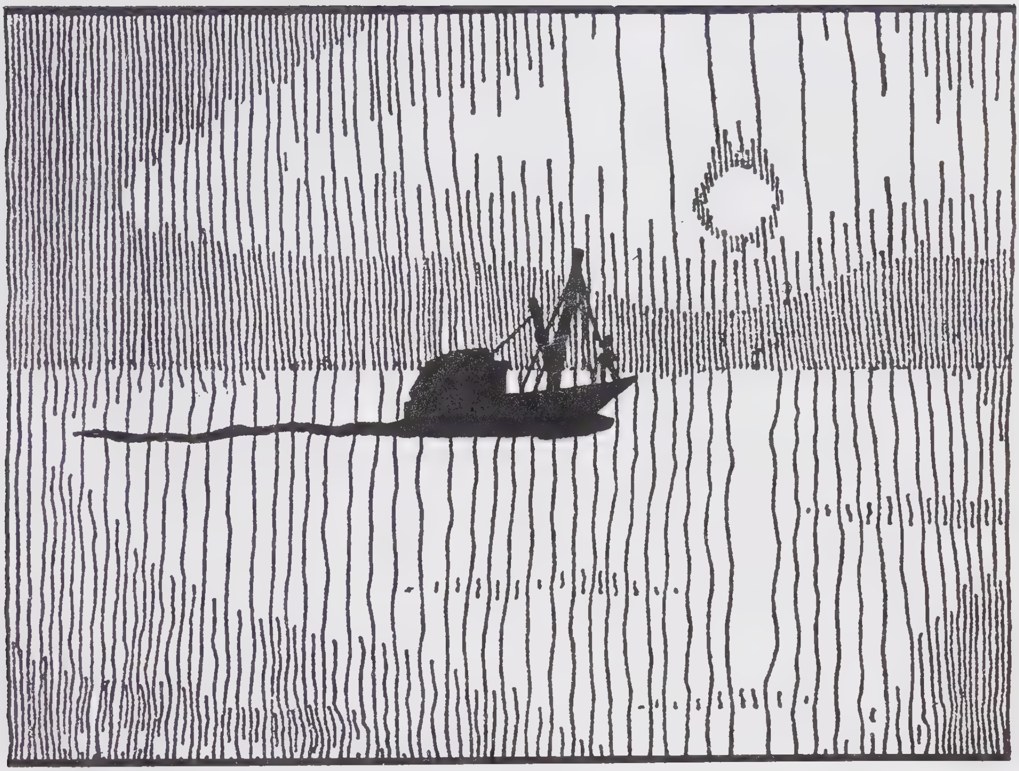

By Greg Knudsen

New Laws Make Waves

by Richard Shomura

Japan is the leading fishing nation in the Pacific with an annual catch that in recent years has been on the order of 10 million metric tons. In 1977, the catch reached 10.7 million tons. Today, Japan and other nations throughout the world are adjusting to a new maritme regime. This adjustment is in response to the move by many nations to extend their jurisdictions over fishery resources to 200 nautical miles from their shorelines. Japan's concern with extended jurisdiction is due to the fact that 40-45% of its total annual catch is taken from within 200 miles of other nations' shores.

Extended Jurisdiction

In comparison with today's complexities, the rules governing the movement and operation of vessels in the high seas before World War II, were simple. Before World War II, the international community generally accepted a 3-mile territorial sea along with specific language to cover passage through straits, definition of bays and so on.

In the Post WWII era, three major events took place to complicate maritime and fishing activities.

The first was a United Nation's Law of the Sea Conference held in 1958. The outcome of this conference resulted in an agreement to a Convention on Fishing.

The second event was the 1964 ratification of the Geneva Convention on the Continental Shelf. This convention established the concept that a coastal state had full jurisdiction over fishery resources which were intimately associated with the shelf all the way out to the edge of the continental shelf. As expected, problems arose on the definition of what constituted a creature of the continental shelf. Futhermore, Japan did not sign the agreement.

The third and most awesome event that started in the 1950's but steamrolled in the 1970's was the unilateral claim of jurisdiction seaward of 12 miles by coastal states. El Salvador claimed a 200-mile territorial sea while Peru, Ecuador and Chile joined forces and established a trilateral maritime zone. The Congress of the United States passed the Fishery Conservation and Management Act of 1976, whereby the U.S. claimed jurisdiction over fishery resources out to 200 nautical miles off its shores. The language of that law however, excluded tuna from this jurisdiction.

ESTIMATED CATCHES BY JAPANESE, TAIWANESE, AND KOREAN LONGLINERS FROM THE 200-MILE ZONES OF SPC MEMBER NATIONS. FROM THE BOOK, THE POLITICS OF PACIFIC ISLANDS FISHERIES BY GEORGE KENT.

	1973	1974	1975	1976
American Samoa	404	19	496	387
Cook Islands	1107	361	3812	2866
Fiji	818	303	281	1554
French Polynesia	5658	5266	7044	7265
Kiribati	4368	4044	12091	11348
Guam & Trust Territory	16692	19860	20166	20602
Tonga	158	29	82	817
Nauru	1407	1101	948	1844
New Caledonia	4617	1585	1689	1801
Vanuatu	1758	432	448	1012
Niue	69	10	5	289
Norfolk Island	812	419	312	700
Papua New Guinea	14104	7039	3810	6313
Pitcairn Island	1251	1209	513	1089
Solomon Islands	6825	2875	1279	2709
Tokelau	764	25	1034	449
Tuvalu	1186	174	2205	1886
Wallis and Futuna	513	57	189	386
Western Samoa	264	11	133	160
Howland, Baker, Palmyra, and Jarvis Islands	1059	1396	3588	3152

(metric tons)

The U.S. position was that tuna, being highly migratory, could best be protected through an international forum. Since the U.S. move, other countries have established their own 200-mile legislation.

Japan's Situation

Obviously for a nation such as Japan, which depends upon getting 45% of its catch from someone elses 200-mile zone, the FCZ-EEZ (Fishery Conservation Zone - Exclusive Economic Zone) poses problems of major dimensions. What action has Japan taken to counter this move by the international community? While recognizing the fact that the current series of Law of the Sea meetings is still trying to resolve the problems created by the extended jurisdiction, it appears to be a reality and an accepted fact. When Japan realized that extended jurisdiction would not go away, steps were taken to protect Japan's waters from neighboring countries which had already established extended jurisdiction zones, out to provide access to 200-mile zones of countries with resources important to Japan. Tuna fishing access agreements were signed with Australia, Papua New Guinea, the Trust Territory of the Pacific Islands and Kiribati. Squid agreements were also made with New Zealand.

Japan developed fisheries in foreign countries by (A) buying into domestic fishing companies (B) forming trading companies and (C) by establishing joint ventures. For example, Japan's joint-venture in the Solomon Islands includes catcher vessels, shoreside facilities, a cannery and so on.

Photos by George Kent

Developing profitable fishing industries and canneries through joint ventures and other cooperative efforts are important goals of many countries in the Pacific.

Technical assistance and aid is offered by Japan to interested Pacific Island nations. Japan was already moving in this direction even before the flurry of extended jurisdiction activity. It makes good sense to provide aid and technical assistance to developing countries if one wants to have access to the resources of that country. Japan has also provided financial backing to international fishery organizations such as the Southeast Asian Fishery Development Center. In addition to funds, Japan also provides technical assistance to these organizations.

In Western Samoa, Japan is providing the funds to develop the harbor infrastructure for fisheries, funding the construction of the fisheries building in Apia and also providing technical aid. In Tonga, Japan has a project to assist in developing a tuna bait fishery. Japan also has the equivalent of the U.S. Peace Corps program with specialists helping in the area of fisheries.

Although Japan is recognized as the leader in aquaculture, recent developments suggest that the plan to increase their efforts is in this field. Part of this move is based on the premise that Japan will find it difficult obtaining access to natural stocks in coastal waters of other countries.

Finally, Japan is looking at new resources for exploration. For the last several years, Japan has sent major expeditions to the Antarctic to see if krill can be caught in commercial quantities. Krill are small shrimp-like animals that form the main diet of whales. Now that the whale populations are down, the krill resources may be under-utilized. Other potential resources include squid, sauries and possibly other deep-water species. Undoubtedly, Japan will be looking at these resources also.

There is no question that Japan has played a major role in fisheries in the Post-WWII years. I expect Japan to continue as a leader in the extended jurisdicition era.

Appendix 1.3

U.S.A. FISHERY CONSERVATION AND MANAGEMENT ACT OF 1976 AND ITS RESEARCH REQUIREMENTS

by

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1. INTRODUCTION

The Fishery Conservation and Management Act (FCMA) promulgated by the United States of America in 1976 changed the perception of the role that the U.S.A. should play in the utilization of the fishery resources found within 200 mi of U.S. shores. There is currently a general mood and movement in the U.S.A. to take a more active role in the harvesting of these resources and to enact management regimes which would incorporate maximum domestic harvesting within an "optimum" yield framework.

The following section provides a brief summary of the FCMA followed by some general comments relating to fisheries research under the FCMA.

2. FISHERY CONSERVATION AND MANAGEMENT ACT OF 1976 (From U.S. Department of Commerce, 1979:xv-xvi)

The Fishery Conservation and Management Act of 1976 (FCMA), Public Law 94-265, signed on 13 April 1976, provides for the conservation and exclusive management of all fishery resources within the U.S. fishery conservation zone (FCZ), except highly migratory species of tuna. It also provides for exclusive management authority over Continental Shelf fishery resources and over anadromous species beyond the U.S. FCZ, except during the time they are found within any foreign nation's territorial sea or fishery conservation zone (or the equivalent), to the extent that such sea or zone is recognized by the United States.

The U.S. FCZ extends from the seaward boundaries of the territorial sea (3 n mi from shore for all but two states) to 200 n mi from shore. The seaward boundaries of Texas and the Gulf Coast of Florida are 3 marine leagues (9 n mi).

2.1 Governing International Fishery Agreements

Under the FCMA, the U.S. Department of State, with cooperation from the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce, negotiates a Governing International Fishery Agreement (GIFA) with foreign countries wishing to fish within the U.S. FCZ. After the GIFA is signed it is transmitted by the President to the Congress for review.

2.2 Foreign Fishing Permit

After a GIFA is in force, the foreign nation submits a vessel permit application for each vessel to the U.S. Department of State. The U.S. Department of State provides copies of the application to the Congress, the U.S. Coast Guard, the appropriate Regional Fishery Management Council and a copy with recommendations to the Assistant Administrator for Fisheries of NMFS. NMFS also receives recommendations from the Regional Fishery Management Councils and the U.S. Coast Guard.

The Assistant Administrator for Fisheries of NMFS reviews all recommendations pertinent to the application and, after consultation with the U.S. Department of State and the U.S.

Coast Guard, may approve the application. The conditions and restrictions on the approval of the application, and the request for fees, are sent to the foreign nation through the U.S. Department of State.

Vessel permits are prepared by NMFS and transmitted through the Department of State to the foreign nation.

2.3 Fees

Foreign nations (except Canada) engaged in fisheries subject to U.S. jurisdiction are charged permit fees, a poundage fee, a foreign fee surcharge, and an observer fee.

The permit fees are annual charges of U.S.$ 1 per gross registered ton for each vessel engaged in fishing; U.S.$ 0.50 per gross registered ton for each vessel engaged in processing fish (not to exceed U.S.$ 2 500 per vessel); U.S.$ 200 for each ship assisting other vessels in harvesting or processing; and U.S.$ 200 for each vessel in a nonretention fishery.

The poundage fee is computed by taking 3.5 percent of the dockside (ex-vessel) price of fish that are allocated annually to each foreign nation. The value of the fish is based on the dockside price received by U.S. fishermen. For species not landed in the United States, an appropriate foreign dockside price is used. Upon application by a foreign nation at the end of the year, a refund is made for the unused allocations.

Beginning in 1979, there will be a surcharge of up to 20 percent on each nation's permit fee and poundage fee, but not on the observer fee. The surcharge is used to capitalize a fund to compensate U.S. fishermen operating in the U.S. FCZ whose vessels are lost or damaged because of foreign vessel activities, or whose fishing gear is lost or damaged by any foreign or domestic vessel or by "Acts of God". The surcharge is in two instalments. The first instalment is 10 percent, and is payable when the permit fee and poundage fee are paid. The amount of the second instalment will be reduced or waived if actual claims experience indicates that the total of claims against the fund is not as high as estimated.

The observer fee covers U.S. costs including salary, per diem, transportation, and overheads for U.S. observers on board foreign vessels. The fee is computed on the basis of actual observer trips.

2.4 Foreign Allocations

The total allowable level of foreign fishing (TALFF), if any, for any fishery subject to the exclusive fishery management authority of the United States, is that portion of the optimum yield (OY) of such fishery that will not be harvested by vessels of the United States.

Each assessment of OY and each assessment of the anticipated U.S. harvest will be reviewed during each fishing season. Adjustments to TALFFs will be made based on updated information relating to status of stocks, estimated and actual performance of domestic and foreign fleets, and other relevant factors.

2.5 Preliminary Fishery Management Plans (PMPs)

If a foreign nation that has entered into a Governing International Fishery Agreement (GIFA) with the United States applies for permission to fish within the U.S. FCZ, the Secretary of Commerce is empowered to prepare and implement a PMP. PMPs apply only to foreign fishermen, and generally remain in effect until an FMP, prepared by the appropriate Regional Fishery Management Council, goes into effect. As of 20 March 1979, the following PMPs were in effect:

Atlantic PMPs

Atlantic Billfishes and Sharks (43 FR 3818, 27 January 1978)
Hake Fisheries of the Northwestern Atlantic (42 FR 10146, 18 February 1977)

Finfish Caught Incidental to the Foreign Trawl Fisheries of the Northwestern Atlantic (42 FR 9950, 17 February 1977)
Mackerel Fishery of the Northwestern Atlantic (42 FR 9552, 16 February 1977)
Squid Fisheries of the Northwestern Atlantic (42 FR 9597, 16 February 1977)

Pacific PMPs

Sablefish Fishery of the Eastern Bering Sea and the Northeastern Pacific (42 FR 8534, 10 February 1977)
Seamount Groundfish Fishery of the Pacific (42 FR 8568, 10 February 1977)
Shrimp of the Eastern Bering Sea and Gulf of Alaska (42 FR 12386, 3 March 1977)
Snail Fishery of the Eastern Bering Sea (42 FR 9334, 15 February 1977)
Trawl Fisheries and Herring Gillnet Fishery of the Eastern Bering Sea and Northeast Pacific (42 FR 9298, 15 February 1977)
Trawl Fisheries of Washington, Oregon, and California (42 FR 8578, 10 February 1977)

2.6 Fishery Management Plans (FMPs)

The FCMA requires that Regional Fishery Management Councils (and in certain cases, the Secretary of Commerce) prepare FMPs, and that the Secretary of Commerce approve and implement them. Each Council is authorized to prepare FMPs on fisheries within its geographical area of authority.

The Secretary of Commerce has the general responsibility under the Act to implement any FMP or amendment approved or prepared by the Secretary. The Secretary may promulgate such regulations as may be necessary to implement any approved FMP. Enforcement of the FCMA, including the provisions of approved management plans and regulations, is a joint responsibility of the Secretary of Commerce and the Secretary of the department in which the U.S. Coast Guard is operating.

Both foreign and domestic fishing is controlled under FMPs. Currently, foreign fishing is allowed in only two of the FMPs - Commercial Tanner Crab off the Coast of Alaska and Groundfish of the Gulf of Alaska.

As of 20 March 1979, the FMPs listed below were in force.

Atlantic FMPs

Atlantic Groundfish Plan for Haddock, Cod, and Yellowtail Flounder (42 FR 14002, 14 March 1977)
Atlantic Herring Fishery of the Northwestern Atlantic (43 FR 60479, 28 December 1978)
Stone Crab Fishery of the Gulf of Mexico (44 FR 18031, 26 March 1979)
Surf Clam and Ocean Quahog Fisheries (42 FR 60439, 25 November 1977)

Pacific FMPs

Commercial and Recreational Salmon Fisheries off the Coasts of Washington, Oregon and California (42 FR 2142, 26 April 1977)
Northern Anchovy Fishery (43 FR 31655, 21 July 1978)
Groundfish of the Gulf of Alaska (43 FR 17242, 21 April 1978)
Commercial Tanner Crab off the Coast of Alaska (43 FR 21175, 16 May 1978)

3. FISHERY RESEARCH ACTIVITIES

Prior to the passage of the Act in 1976, fisheries research effort in the U.S.A. was directed toward a wide range of fisheries problems, e.g., exploratory fishing, life history studies, monitoring of commercial fisheries, fishery technology, and fish-environment studies. Except in cases where fisheries laboratories worked on management problems as part of U.S.A. commitments as a member of an international organization, e.g., International Commission for Northwest Atlantic Fisheries, research on stock assessment and management by research units in the U.S.A. was minimal in the pre-FCMA period.

Passage of FCMA has forced a reassessment of the research role of these fisheries units. In order to meet the need for management of the fishery resources in the U.S. FCZ, fishery administrators have had to review data needs for existing commercial and recreational fisheries and for socio-economic research and fisheries development.

3.1 Current Commercial Fisheries

In 1977 the U.S.A. was faced with a high-priority need to determine the status of stocks of resources being harvested with the FCZ by foreign fishing vessels. This was necessary in order to establish catch limits for foreign fisheries operating within the 200-mi FCZ.

Many of the fisheries laboratories within the National Marine Fisheries Service thus had to reassess their research activities and in some cases to redirect effort toward stock assessment of fishery resources harvested by domestic and foreign fleets.

3.2 Recreational Fisheries

In the development of fishery management plans, researchers found a wide range in the quality and quantity of commercial catch statistics. In most instances some data are available. This was not true for recreational fishing data. With the exception of the situation in some areas, e.g., California, the recreational catch and effort statistics were generally lacking throughout the U.S.A. For most states, there is currently no reporting requirements for recreational fish catches.

The National Marine Fisheries Service conducted saltwater angling surveys in 1960, 1965 and 1970 through the auspices of the Bureau of the Census. Since the survey depended upon a 1-year recall period, the data incorporated substantial memory bias errors. To correct this shortcoming, NMFS in November 1978 began a marine recreational fisheries survey which includes a combined telephone and on-site intercept survey. Results of this 1-year survey will not be available until February 1980.

3.3 Socio-economic Research

Since management plans require determination of optimum yield which incorporates socio-economic considerations, there has been a major surge of research activities in the area of fishery socio-economics. Currently, a number of socio-economic studies are being undertaken in the U.S.A., especially in areas where fishery management plans are being developed.

3.4 Fisheries Development

One of the goals under the FCMA is to increase the U.S.A. share of the total allowable harvest of resources located within the FCZ. In 1979 the Administration enunciated a positive Federal policy on fisheries development to strengthen the fishing industry in the U.S.A. through a programme based on industry leadership and active Federal support. Currently details of implementing this fishery development programme are being developed. It is expected that Federal fisheries research units will be given the task of determining "first-cut" assessments of resources under consideration in this programme to assist in fishery development and to formulate the basis for subsequent management decisions.

4. REFERENCE

U.S. Department of Commerce, Fisheries of the United States, 1978. Current fishery statis-
1979 tics No. 7800. U.S. Gov.Print.Off., Wash., D.C., 120 p.

8078

SC/SP78/36

Catches of Male and Female Sperm Whales by 2-Degree Square by Japanese Pelagic Whaling Fleets in the North Pacific, 1966-77

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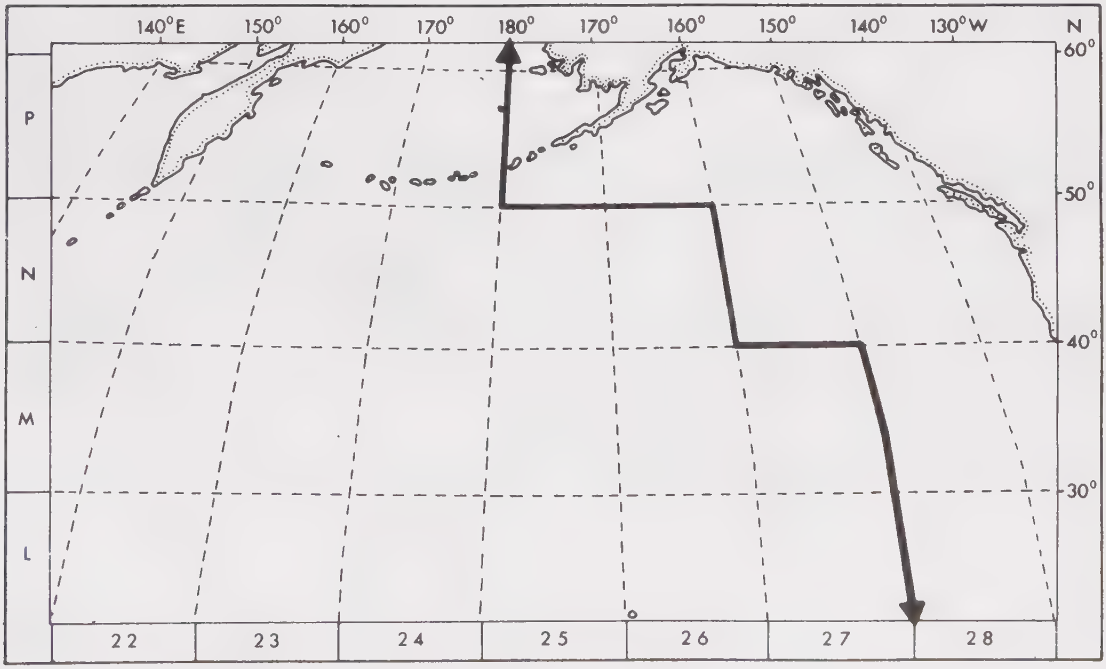
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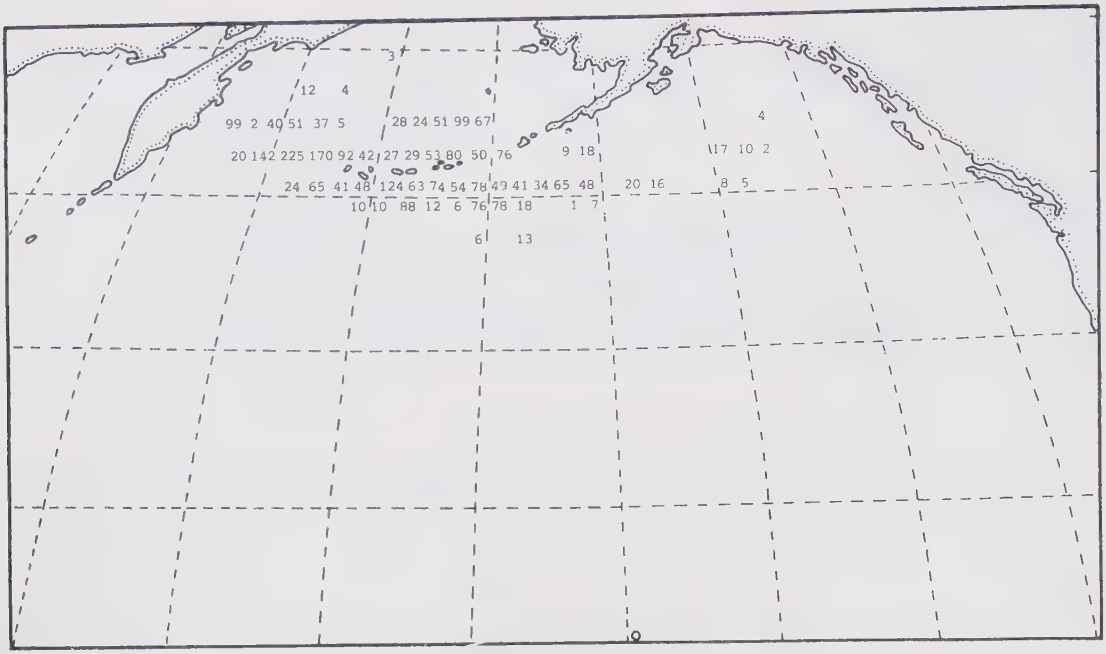
Fig. 1. Map of the North Pacific showing the boundary between Eastern and Western Divisions adopted by the IWC in 1978.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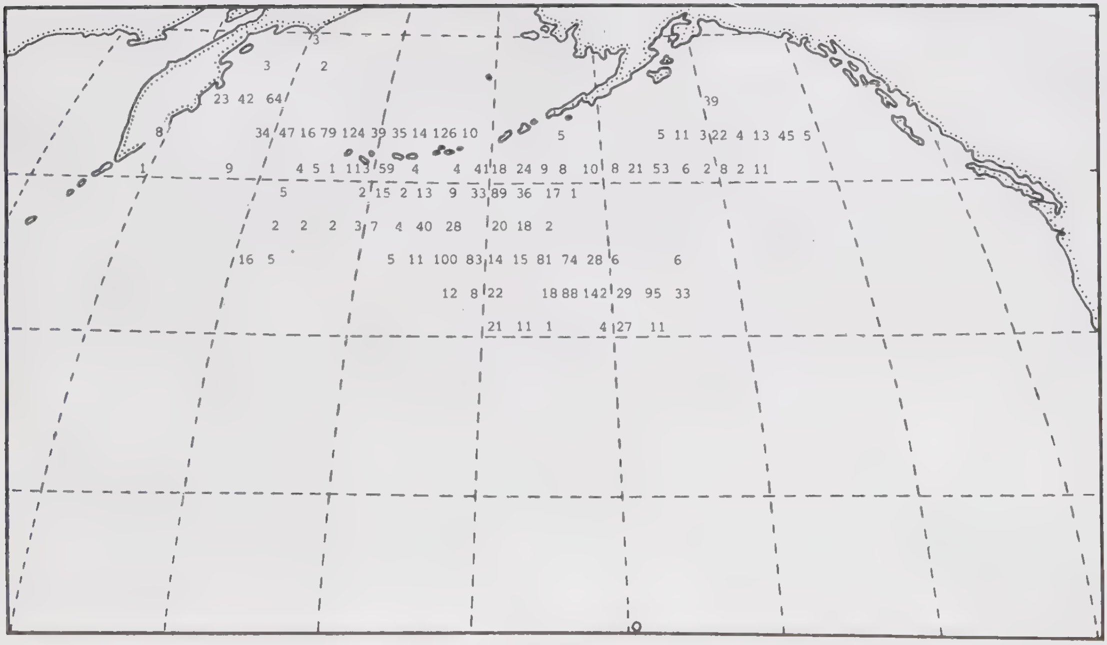
20 142 225 170 92 42 27 29 53 80 50 76 9 18 17 10 2 4
24 65 41 48 124 63 74 54 78 49 41 34 65 48 20 16 8 5
10 10 88 12 6 76 78 18 1 7
6 13

Fig. 2. Catch of male sperm whales in each 2-degree square for 1966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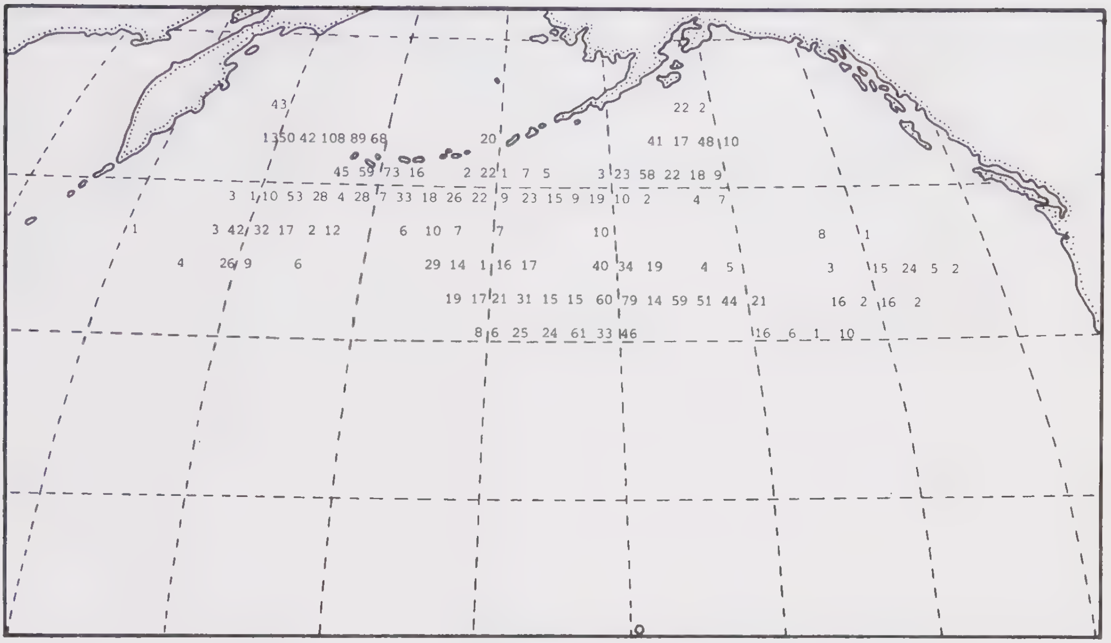
2 2 2 3 7 4 40 28 20 18 2
16 5 5 11 100 83 14 15 81 74 28 6 6
12 8 22 18 88 142 29 95 33
21 11 1 4 27 11

Fig. 3. Catch of male sperm whales in each 2-degree square for 1967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4 7
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3 42 32 17 2 12
6 10 7
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29 14 1 16 17
40 34 19
4 5
3
15 24 5 2
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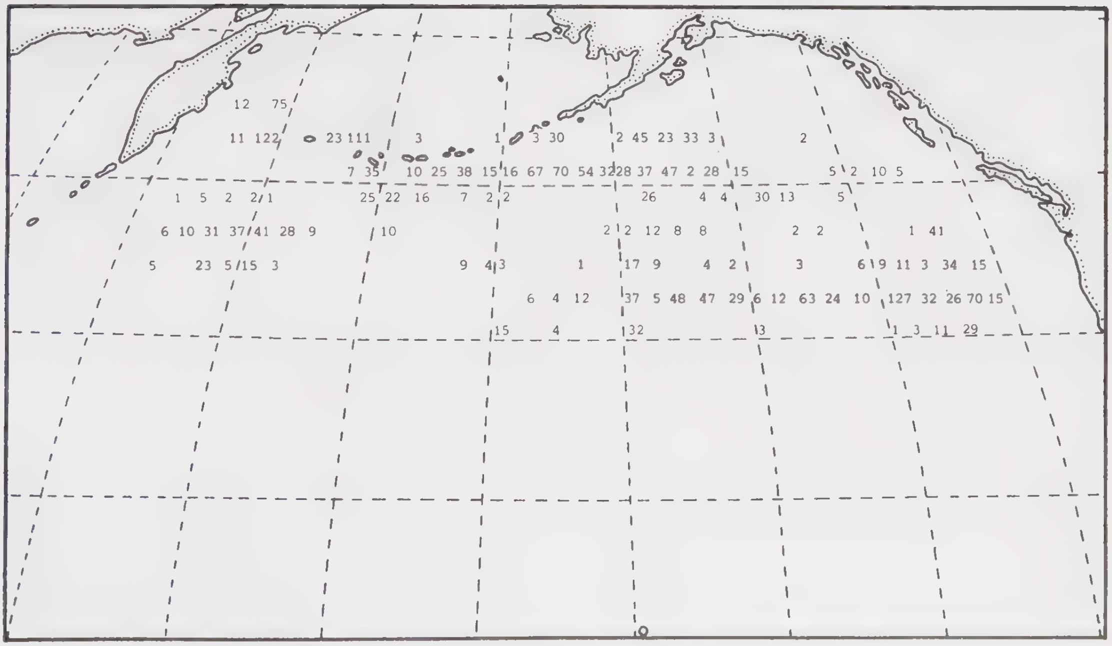
16 2 16 2
8 6 25 24 61 33 46
16 6 1 10

Fig. 4. Catch of male sperm whales in each 2-degree square for 1968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5 2 10 5
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25 22 16
7 2 2
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4 4
30 13
5
6 10 31 37 41 28 9
10
2 2 12 8 8
2 2
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6 9 11 3 34 15
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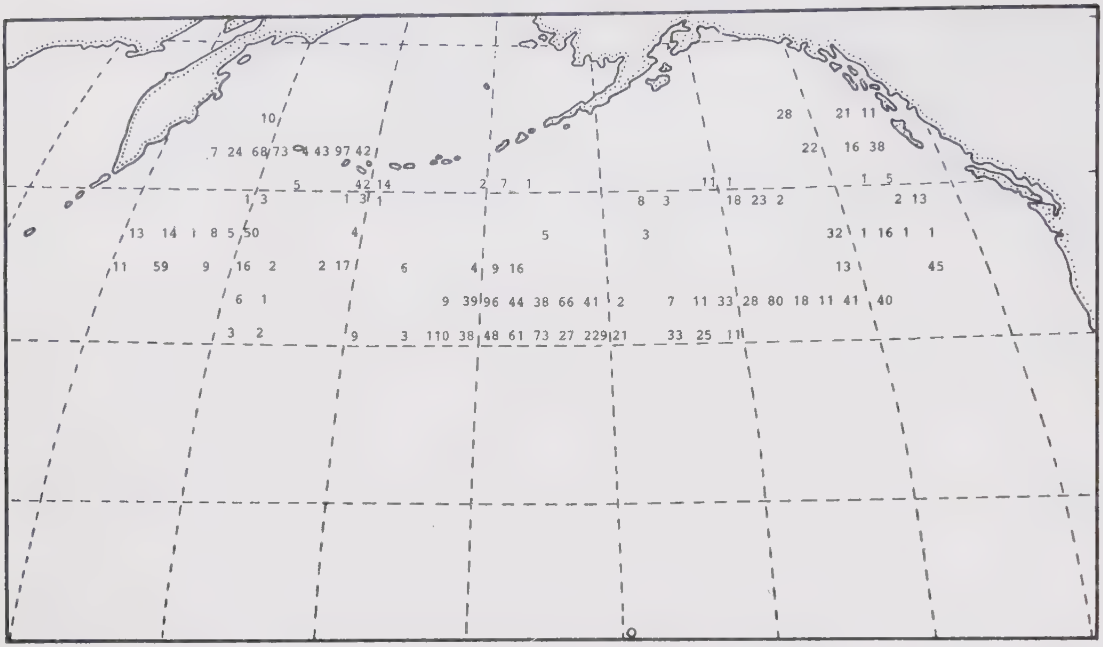
Fig. 5. Catch of male sperm whales in each 2-degree square for 1969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1 3 1 3 1 8 3 18 23 2 2 13
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11 59 9 16 2 2 17 6 4 9 16 13 45
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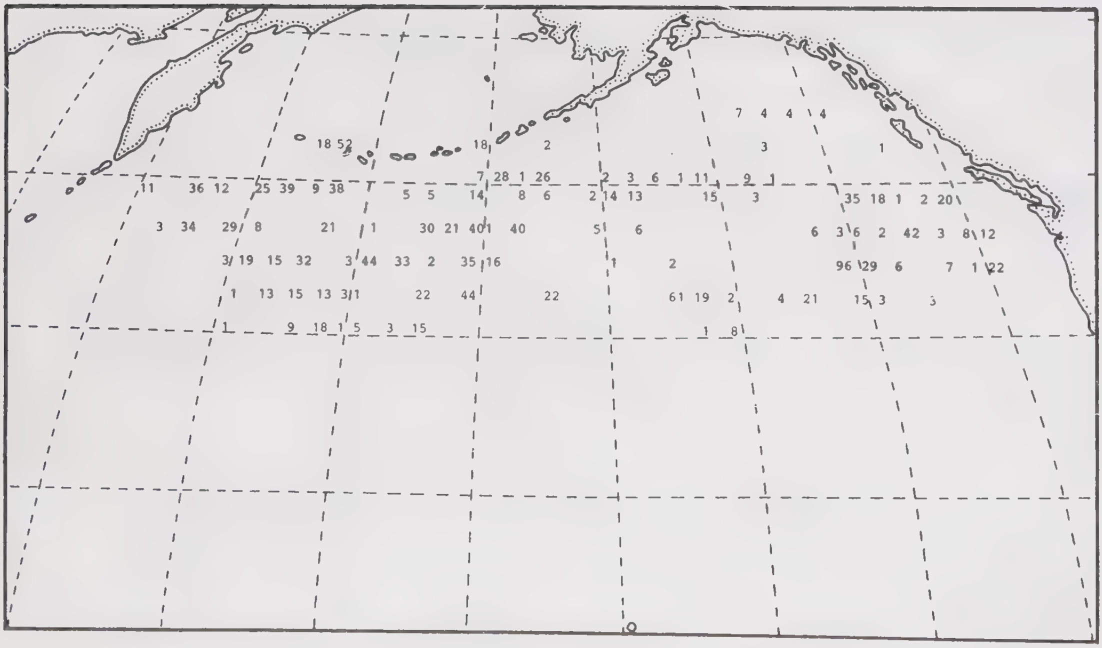
Fig. 6. Catch of male sperm whales in each 2-degree square for 1970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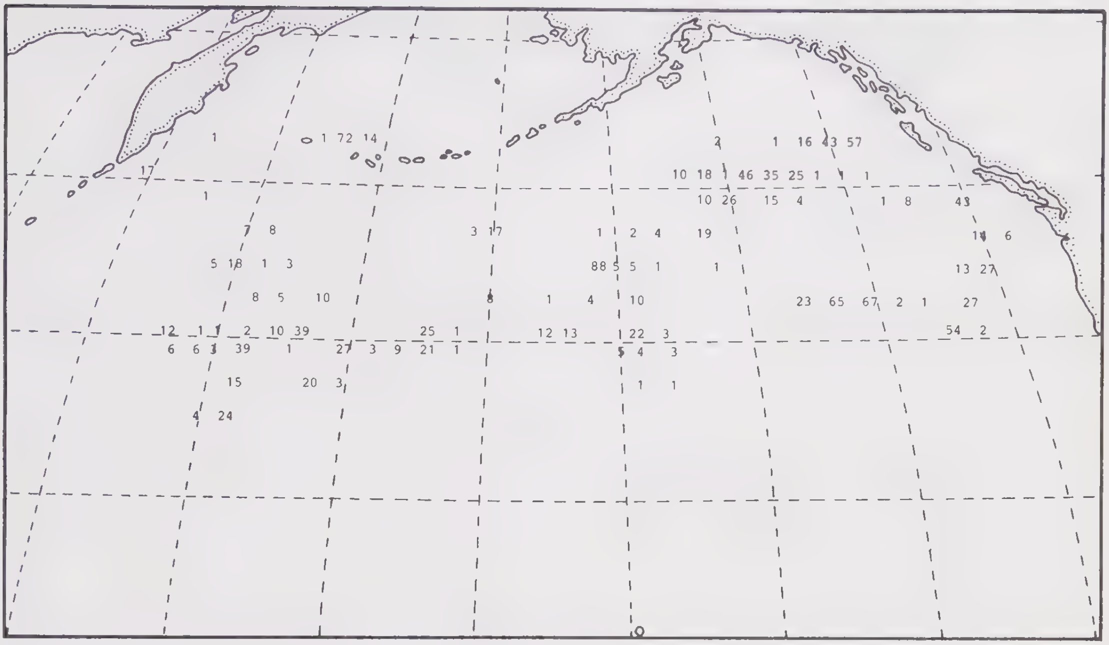
1 9 18 1 5 3 15 1 8

Fig. 7. Catch of male sperm whales in each 2-degree square for 1971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2 1 16 43 57
17
10 18 1 46 35 25 1 1 1
1
10 26 15 4 1 8 43
7 8
3 17
1 2 4
19
14 6
5 18 1 3
88 5 5 1
1
13 27
8 5 10
8
1 4 10
23 65 67 2 1
27
12 1 1 2 10 39
25 1
12 13
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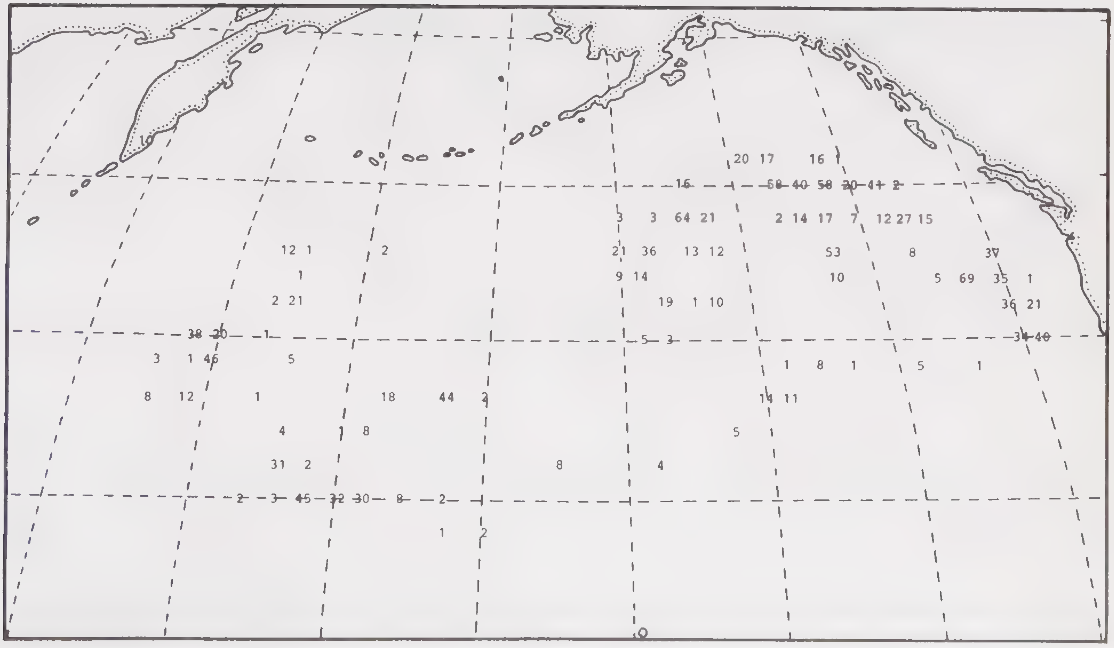
15
20 3
1 1
4 24

Fig. 8. Catch of male sperm whales in each 2-degree square for 1972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5 69 35 1
2 21
19 1 10
36 21
38 20 1
5 3
34 40
3 1 46
5
1 8 1
5
1
8 12
1
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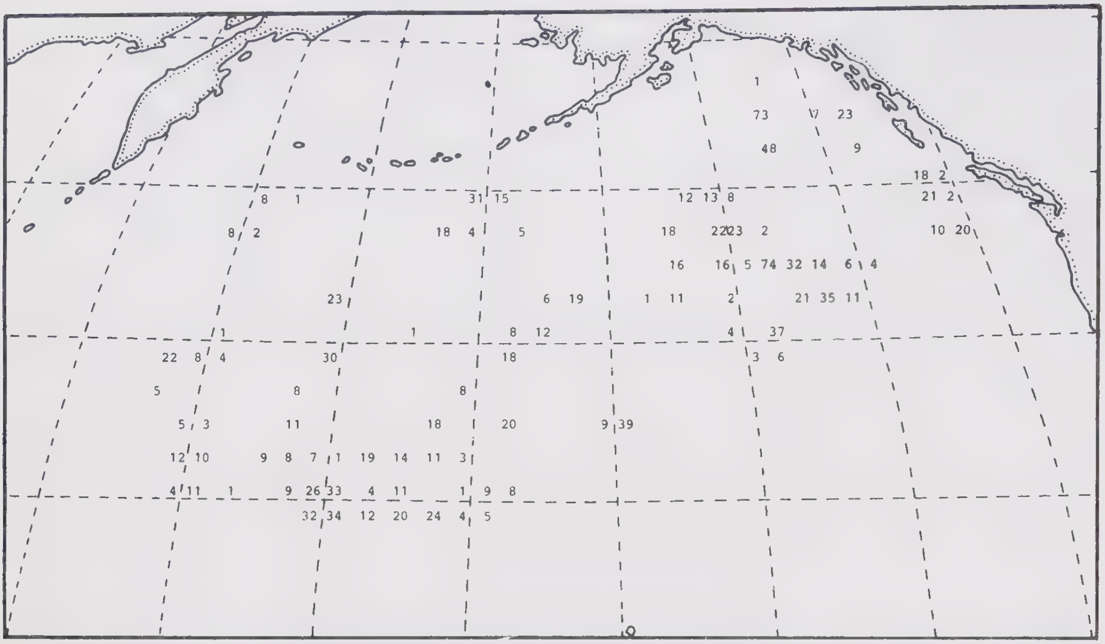
1 2

Fig. 9. Catch of male sperm whales in each 2-degree square for 1973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1 1 8 12 4 37
22 8 4 30 18 3 6
5 8 8
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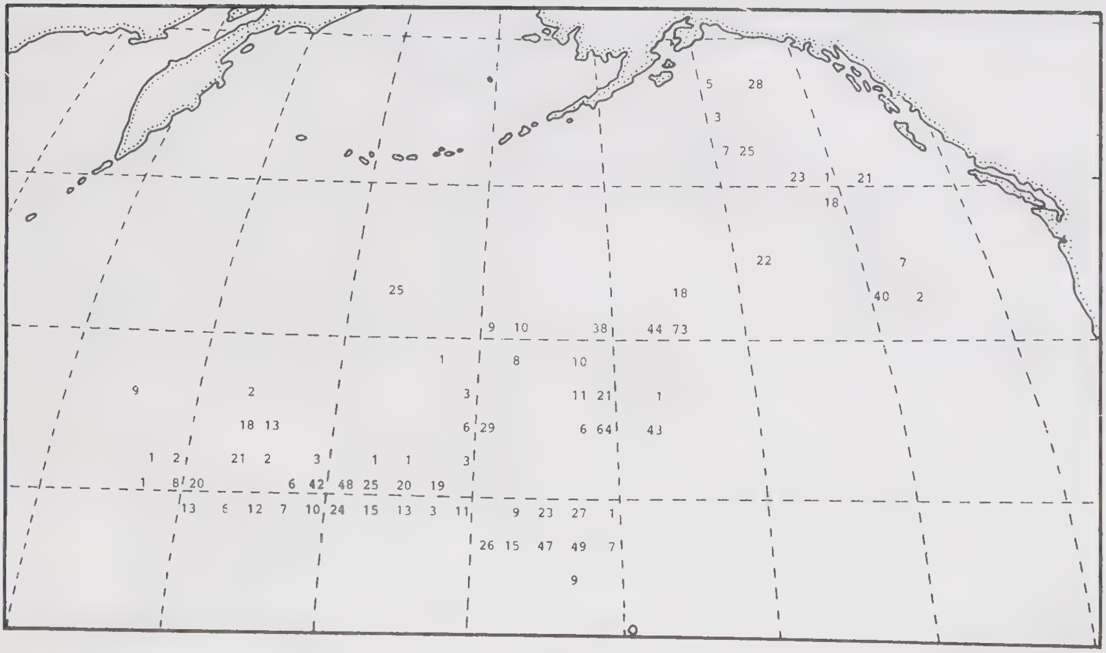
Fig. 10. Catch of male sperm whales in each 2-degree square for 1974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13 6 12 7 10 24 15 13 3 11 9 23 27 1
26 15 47 49 7
9

Fig. 11. Catch of male sperm whales in each 2-degree square for 1975

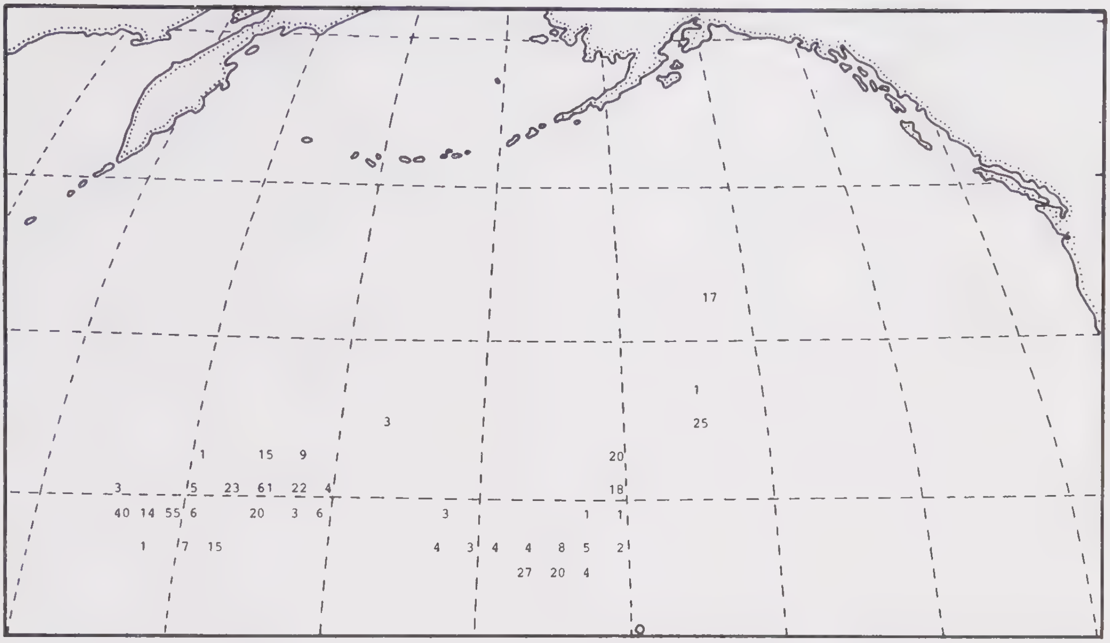
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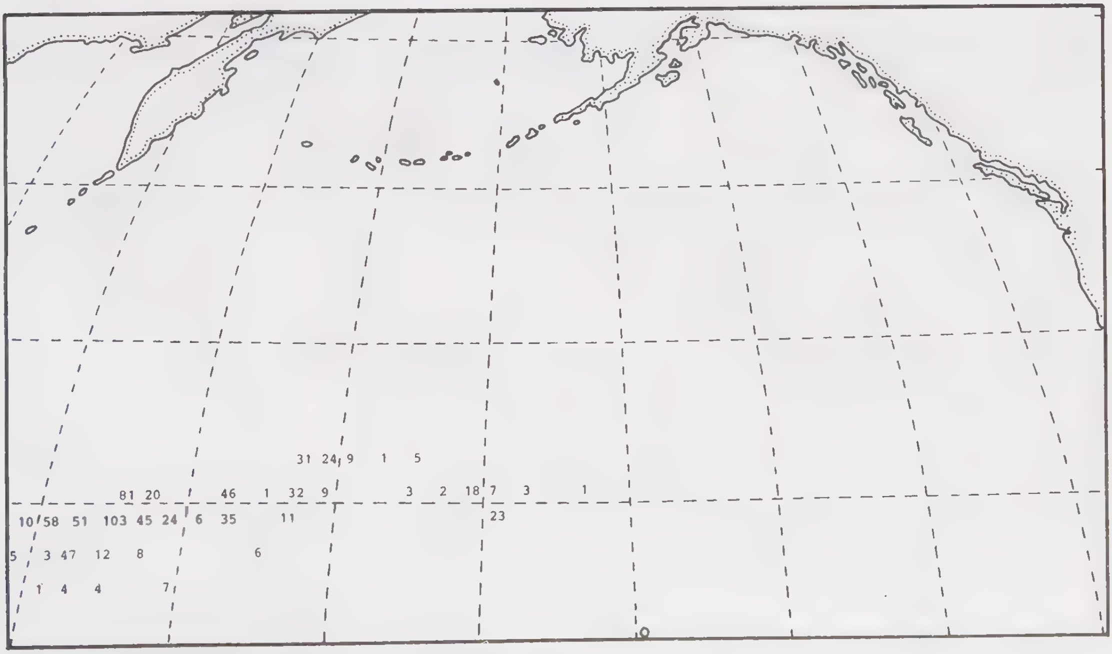
Fig. 12. Catch of male sperm whales in each 2-degree square for 1976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45
24
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Fig. 13. Catch of male sperm whales in each 2-degree square for 1977

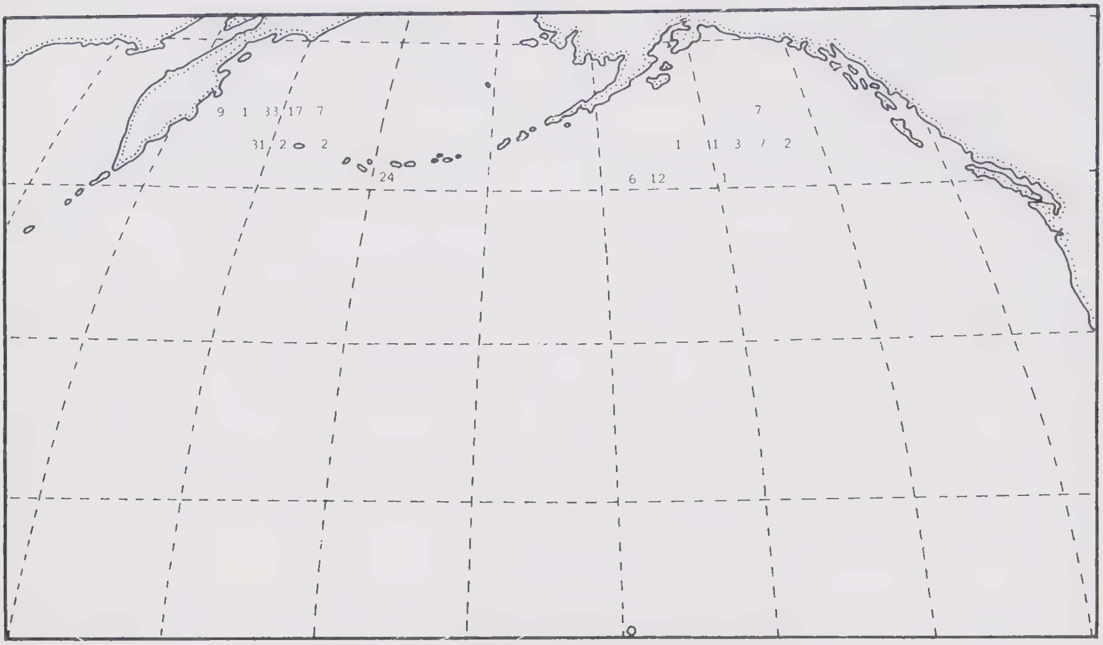
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Fig. 14. Catch of female sperm whales in each 2-degree square for 1966

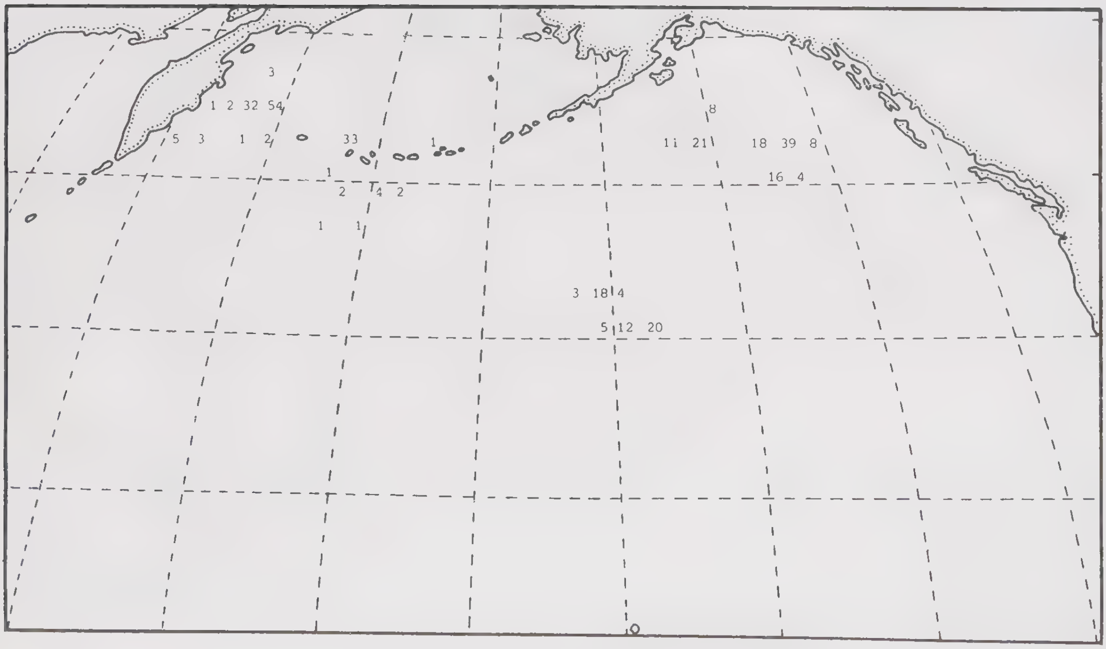
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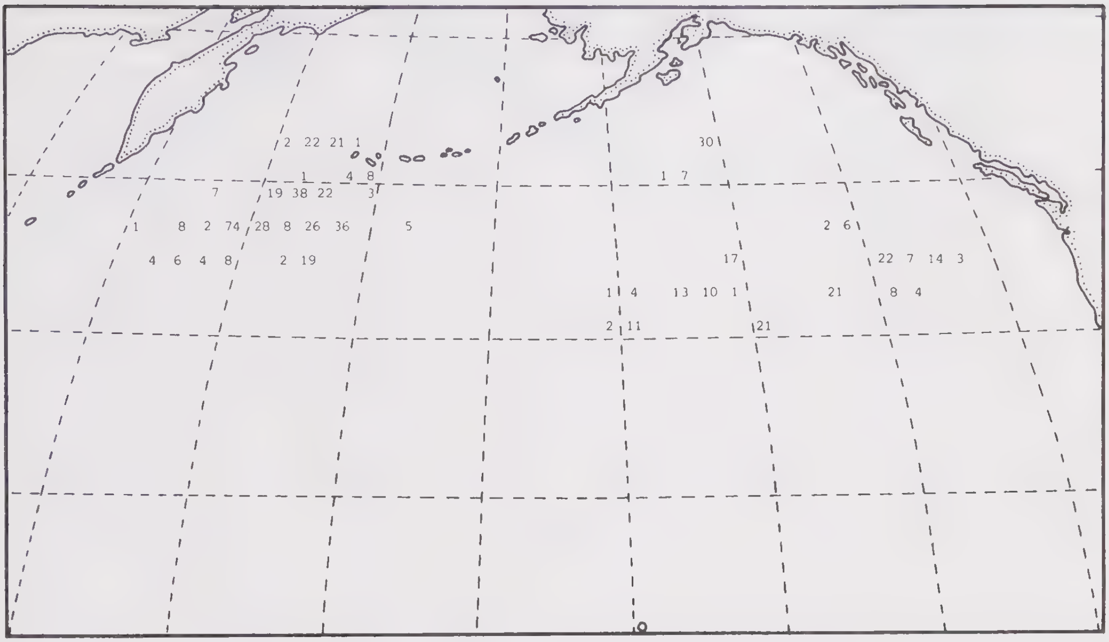
Fig. 15. Catch of female sperm whales in each 2-degree square for 1967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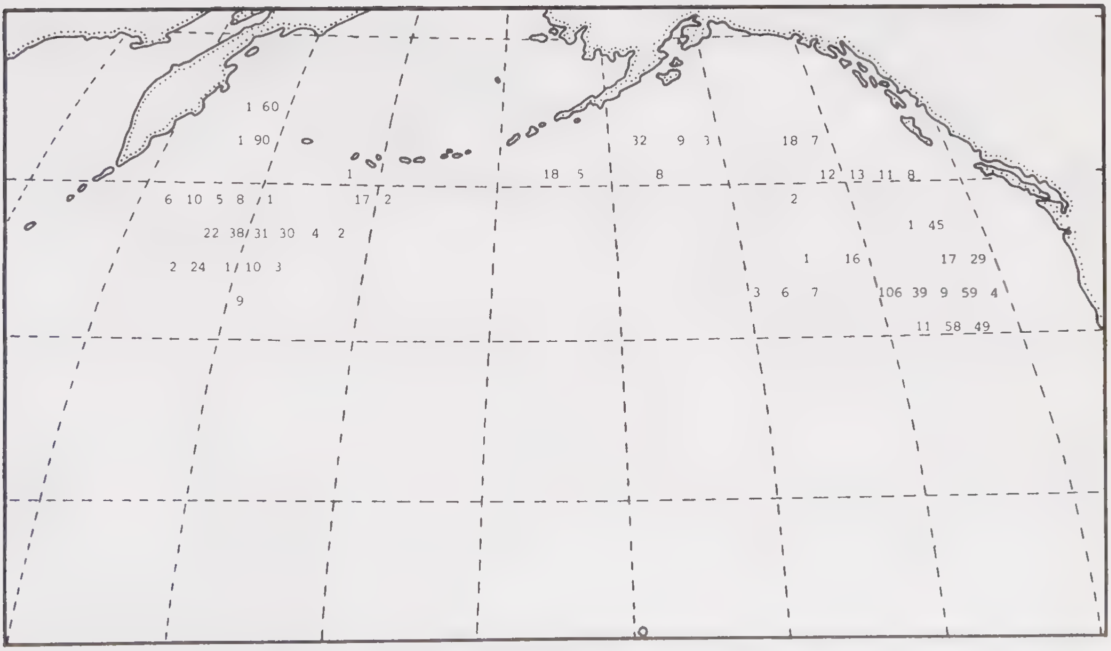
21
8 4
2 11
21

Fig. 16. Catch of female sperm whales in each 2-degree square for 1968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1
17 2
2
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31 30 4 2
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1 16
17 29
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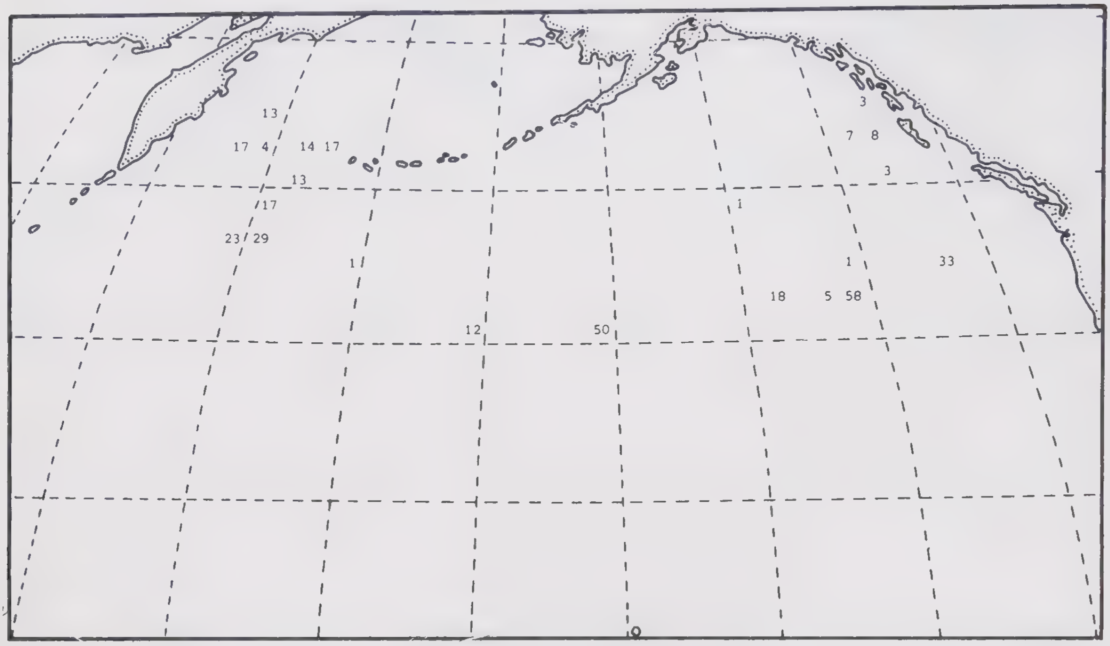
3 6 7
106 39 9 59 4
11 58 49

Fig. 17. Catch of female sperm whales in each 2-degree square for 1969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18
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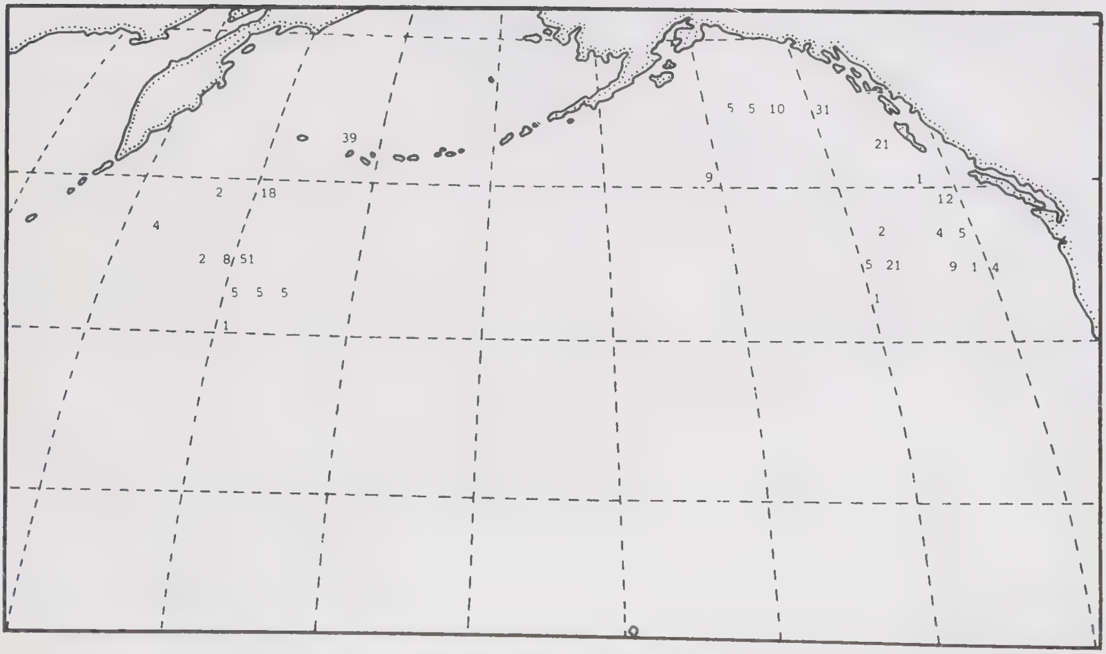
Fig. 18. Catch of female sperm whales in each 2-degree square for 1970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1

Fig. 19. Catch of female sperm whales in each 2-degree square for 1971

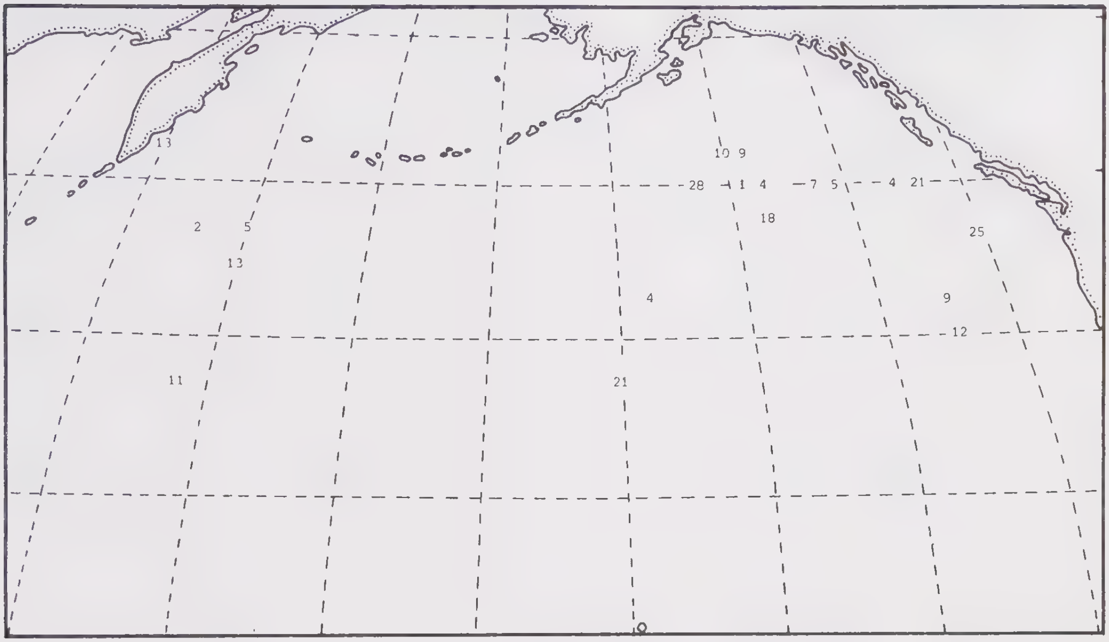
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Fig. 20. Catch of female sperm whales in each 2-degree square for 1972

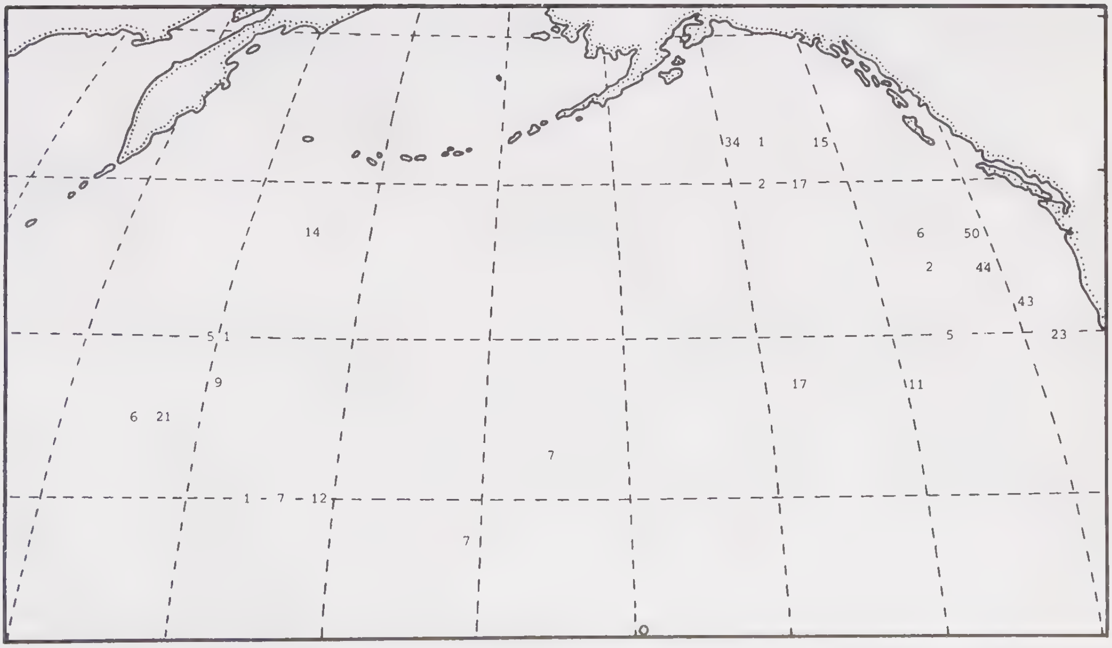
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Fig. 21. Catch of female sperm whales in each 2-degree square for 1973

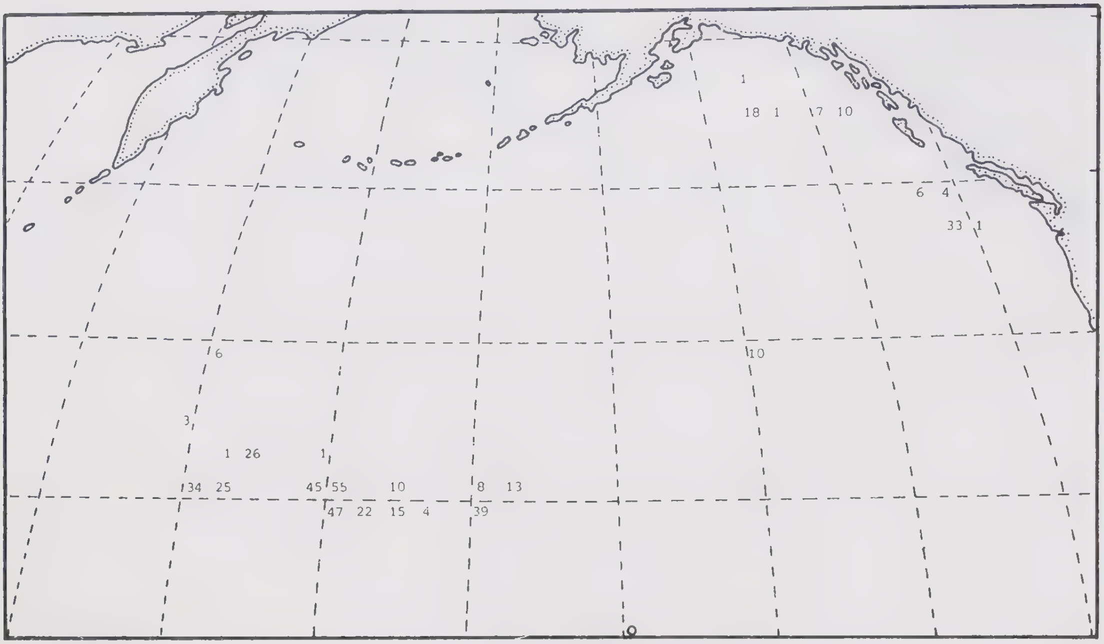
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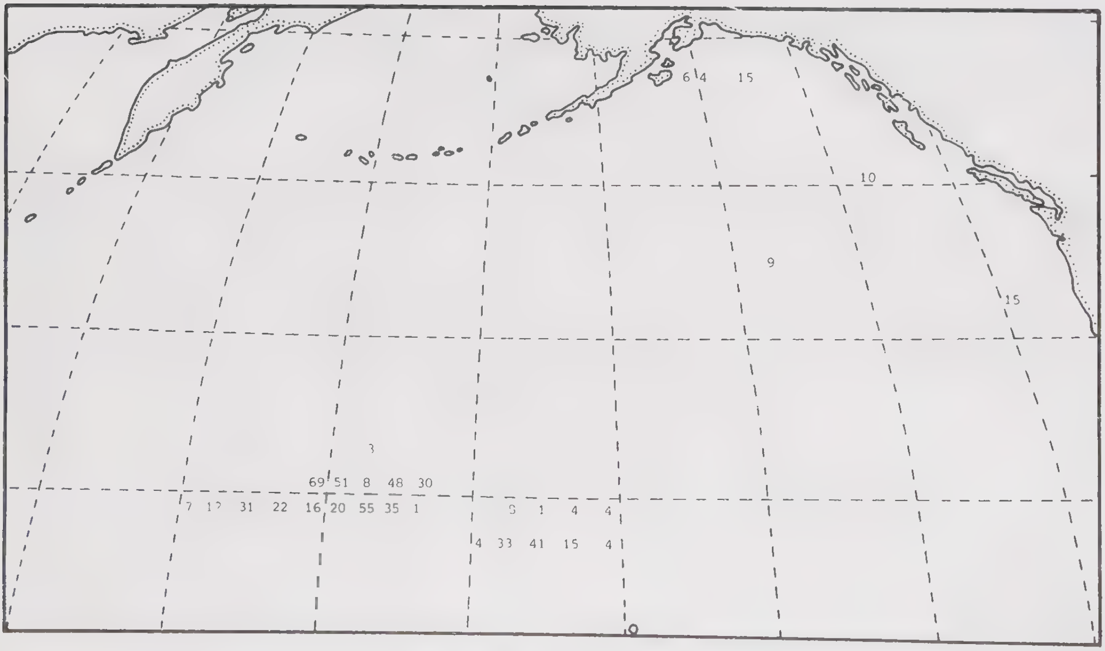
Fig. 22. Catch of female sperm whales in each 2-degree square for 1974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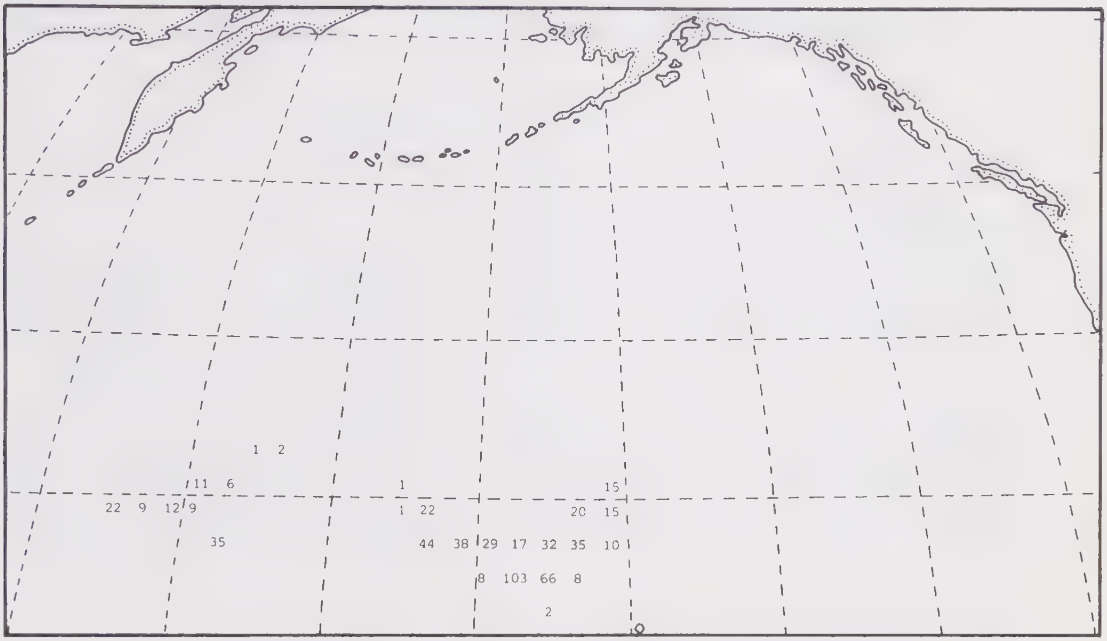
9 1 4 4
4 33 41 15 4

Fig. 23. Catch of female sperm whales in each 2-degree square for 1975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1 22
20 15
35
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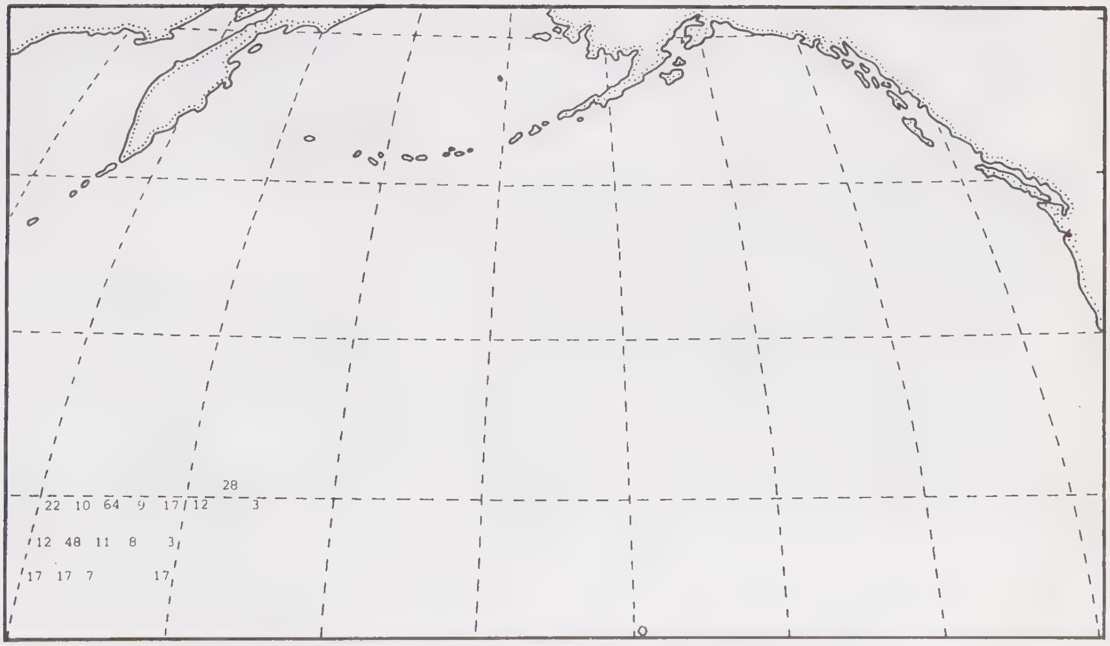
8 103 66 8
2

Fig. 24. Catch of female sperm whales in each 2-degree square for 1976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22 10 64 9 17 12
3
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17 17 7 17

Fig. 25. Catch of female sperm whales in each 2-degree square for 1977

STAUFFER: ESTIMATE OF 1979 NORTHERN ANCHOVY SPAWNING BIOMASS
CalCOFI Rep., Vol. XXI, 1980

ESTIMATE OF THE SPAWNING BIOMASS OF THE NORTHERN ANCHOVY CENTRAL SUBPOPULATION FOR THE 1979-80 FISHING SEASON

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ABSTRACT

The 1979 spawning biomass estimate for the central subpopulation of northern anchovies was 1,723,000 short tons. This estimate is based on the anchovy larva abundance as measured by four egg and larva surveys conducted over the period January-May 1979. Spawning biomass was estimated from larvae abundance using Smith's (1972) method. Based on the Pacific Fishery Management Council's Anchovy Plan (PFMC 1978), optimum yield for the central subpopulation during the 1979-80 season was 241,000 short tons. The optimum yield in the U.S. Fishery Conservation Zone was 168,700 short tons. The 1979-80 U.S. reduction quota was 156,100 short tons.

RESUMEN

En 1979 el cálculo de la biomasa del desove para la subpoblación central de anchoveta del norte fue de 1,564,000 toneladas métricas (1,723,000 toneladas). Este cálculo se basa en la abundancia de larvas de anchoveta que se midió en cuatro cruceros de reconocimiento de huevecillos y larvas efectuados en el periodo enero-mayo de 1979. El cálculo de la biomasa del desove se hizo de la abundancia de larvas usando el método de Smith (1972). Basado en el plan de anchoveta del Pacific Fishery Management Council (PFMC 1978), el rendimiento óptimo de la subpoblación central durante la temporada de 1979-80 fue de 218,630 toneladas métricas (241,000 toneladas). El rendimiento óptimo en la zona de conservación de la pesquería de los EE.UU. fue de 153,041 toneladas métricas (168,700 toneladas). La reducción de la cuota efectuada por los EE. UU. en 1979-80 fue de 141,611 toneladas métricas (156,100 toneladas).

INTRODUCTION

The Fishery Management Plan (FMP) for the Northern Anchovy Fishery (Pacific Fishery Management Council 1978) requires that catch quotas be determined on the basis of current estimates of spawner biomass. The purpose of this paper is to document the 1979 estimate of spawning biomass of the central subpopulation of northern anchovy to establish the optimum yield for the 1979-80 season. The estimate is based on the 1979 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey for the winter and spring quarters. This cooperative survey was conducted under the auspices of the La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service. Scripps Institution of Oceanography (SIO) cooperated in conducting the survey.

The procedure for estimating anchovy spawning biomass from anchovy larva abundance is based on the method given by Smith (1972), as documented in Appendix I of the FMP. In addition, the larva abundance estimate for the 1979 winter and spring quarters was expanded to an annual larva abundance based on the analysis of the historical data.

LARVA SURVEY

The geographic range of the central subpopulation is within the eight regions outlined on the CalCOFI station plan given in Figure 1. For convenience the author redefined those regions off southern California and Baja California in 1979 so that boundaries between the region group 7, 8, and 9 and the region group 11, 13, and 14 coincided with the U.S.-Mexico border. Four plankton surveys were conducted over the range of the central subpopulation during the five months, January through March 1979: 1) 7901 EB, January 12-22; 2) 7903 DS, February 25-March 13; 3) 7904 JD, March 22-April 17; 4) 7905 JD, April 30-May 21. The stations occupied by each cruise are shown in Figure 2. Unfortunately, only two of the four cruises, 7903 and 7905, received permits to conduct fishery research within Mexico's 200-mile zone.

Plankton samples on three of the four cruises were collected with a CalCOFI Bongo net, which is actually a pair of nets with a combined cross-sectional area equal to a CalCOFI 1-meter ring net. The 1-meter ring net was used on the first cruise, 7901. Station data and plankton samples were brought back to the Southwest Fisheries Center for processing and sorting. One-hundred percent of the plankton samples was sorted if the station was beyond 200 miles or if the plankton volume was less than 26 ml; otherwise, a 50% aliquot of the samples was sorted. The 1979 estimate includes station data from only the 118 standard stations defined by Smith (1972) to be those stations routinely occupied since 1951 and within the range of the central subpopulation.

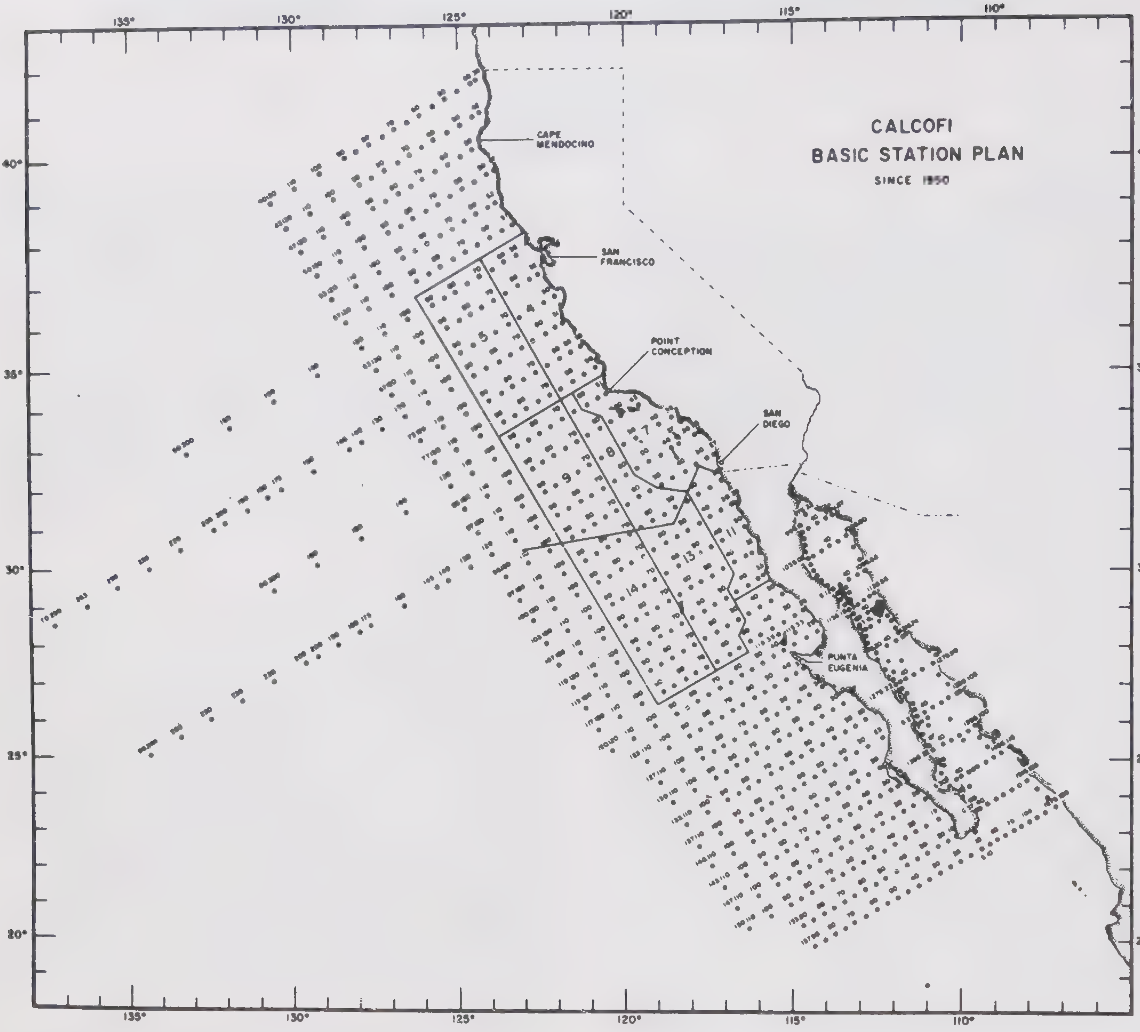
CALCOFI
BASIC STATION PLAN
SINCE 1950
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
135°
130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
4
5
7
8
9
11
13
14

Figure 1. CalCOFI basic station plan. The geographic range of the central subpopulation of northern anchovy is within the eight numbered regions.

SURVEY RESULTS

The distribution of the number of anchovy larvae per plankton net tow for the four cruises that make up the basic data for the 1979 spawning biomass estimate is summarized in Figure 2. In general, evidence of anchovy spawning north of Point Conception in region 4 off cen-

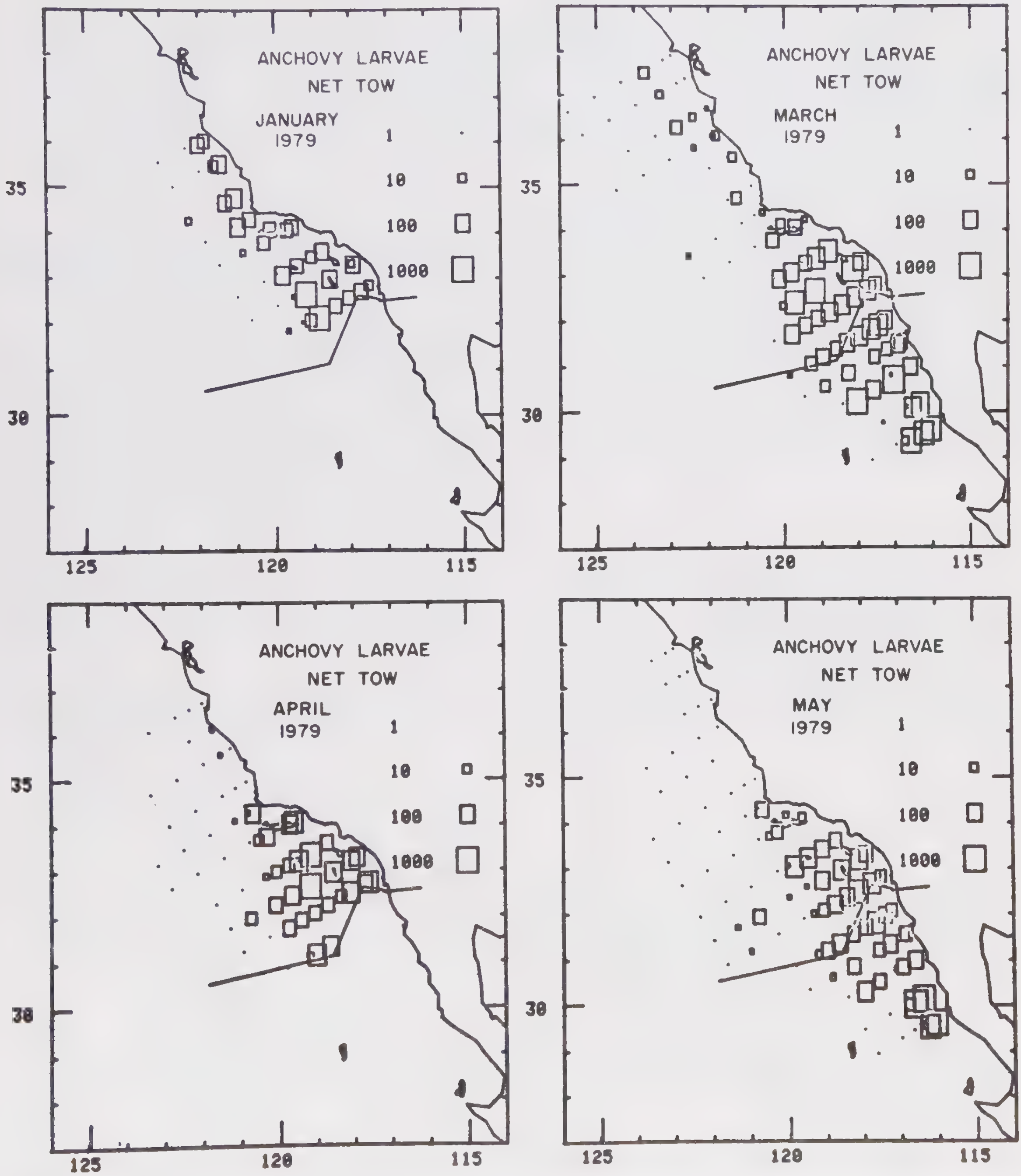
ANCHOVY LARVAE
NET TOW
JANUARY 1979
MARCH 1979
APRIL 1979
MAY 1979
1
10
100
1000
35
30
125
120
115

Figure 2. Pattern of occupied stations for the 1979 cruises and geographic distribution of anchovy larvae for central subpopulation in winter and spring months of 1979 spawning season. The legend is in numbers of larvae per net tow.

tral California was only found during the month of January. To the south, anchovy larvae were consistently taken on all four cruises as far out as 140 nautical miles, approximately 40 nautical miles farther than in 1978. The percent of the larvae south of the U.S.-Mexico border was 53.5% in 1979; the long-term average is 30%. Spawning persisted from January through May off southern California and Baja California.

Because the regions offshore of Baja California were only surveyed in the second half of each quarter, the quarterly larva abundance for the Baja regions 11, 13, and 14 (L_m) was estimated from a linear regression model using an adjusted larva abundance (L_a). Adjusted larva abundance is the larva abundance for the Baja regions 11, 13 and 14 based on the single cruise ($L_{m\frac{1}{2}}$) divided by the ratio of Southern California larva abundance for regions 7, 8, and 9 for the corresponding single cruise ($L_{c\frac{1}{2}}$) to the larva abundance in the same regions for the two cruises averaged together (L_c), i.e.

$$L_a = L_{m\frac{1}{2}} \left(L_c \,/\, L_{c\frac{1}{2}}\right) \text{ and}$$

$$L_m = b_0 + b_1 L_a \qquad (1)$$

This relationship for the adjusted larva abundance is based on the premise that the Baja larva abundance for the single cruise ($L_{m\frac{1}{2}}$) divided by the abundance in the same area for the two cruises averaged together (L_m) is proportional to southern California larva abundance for the corresponding single cruise ($L_{c\frac{1}{2}}$) divided by the abundance in the same area for the two cruises together (L_c), i.e.

$$L_{m\frac{1}{2}} \,/\, L_m \approx L_{c\frac{1}{2}} \,/\, L_c$$

so that

$$L_m \approx L_{m\frac{1}{2}} \left(L_c \,/\, L_{c\frac{1}{2}}\right)$$

The regression model (1) was fit to the historical CalCOFI larva data for only the standard stations and with new region boundaries. The model was fit to winter quarter data from the 15 years, 1951-60, 1966, 1969, 1972, 1975, and 1978, with the following result:

$$L_m = -0.2744 \times 10^{12} + 1.0913 L_a \,;\, R^2 = 0.975 \qquad (2)$$

There were sufficient data for only 13 years, 1951-60, 1966, 1969, and 1978, to fit the model for the spring quarter. The fitted equation is

$$L_m = 0.3860 \times 10^{12} + 0.9108 L_a \,;\, R^2 = 0.627 \qquad (3)$$

The fit of equations (2) and (3) is shown in Figure 3.

For the winter quarter in 1979, L_a equals 2.882×10^{12} larvae and L_m is estimated from equation (2) to be 2.871×10^{12} larvae. This added to the larva abundance north of the U.S.-Mexico border gives a total anchovy larva abundance of 6.546×10^{12} larvae for the winter quarter. For the spring quarter, L_a equals 5.625×10^{12} larvae. The resulting L_m using equation (3) is 5.509×10^{12} larvae. Adding this amount to the northern abundance gives a spring quarter abundance of 9.124×10^{12} larvae. The sum of the two quarterly estimates give a winter-plus-spring larva abundance (L_{ws}) of 15.670×10^{12} larvae. For historical time series, the quarterly and winter-plus-spring larva abundance estimates presented in Table 2 of Appendix I in the FMP (PFMC 1978) are repeated here in Table 1, along with the 1979 values.

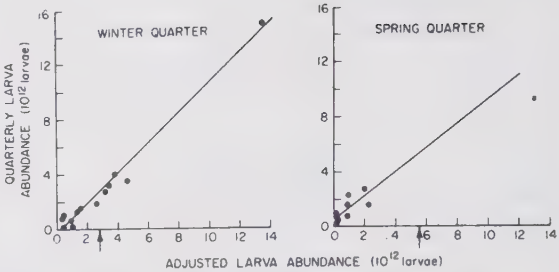

Figure 3. Regression models for estimating larva abundance in Mexico's 200-mile zone for winter and spring quarters from the adjusted larva abundance for the winter and spring quarter as defined in the text; arrows indicate 1979 values.

TABLE 1
Estimated Larva Abundance (10^{12} Larvae) and the Spawner Biomass[1] for the Central Subpopulation[2]

Year	Winter	Spring	Winter and Spring	Annual	Spawner biomass in millions of short tons
1951.....	.298	.690	.988	1.841	.180
1952.....	.407	.457	.864	1.600	.156
1953.....	1.210	.373	1.583	5.208	.510
1954.....	4.469	.988	5.457	7.838	.768
1955.....	5.588	1.709	7.297	8.618	.845
1956.....	1.911	1.206	3.117	4.944	.485
1957.....	5.954	4.308	10.262	11.906	1.167
1958.....	8.114	5.236	13.350	15.087	1.479
1959.....	6.341	8.155	14.496	15.440	1.514
1960.....	7.552	7.547	15.099	15.713	1.540
1961.....	.992	6.714	7.706	11.827	1.159
1962.....	4.814	23.567	28.381	30.478	2.986
1963.....	17.377	24.818	42.195	43.407	4.254
1964.....	8.941	14.383	23.324	29.559	2.901
1965.....	19.155	22.690	41.845	47.540	4.650
1966.....	15.103	15.865	30.968	36.452	3.572
1969.....	19.756	6.538	26.294	30.594	2.998
1972.....	8.213	14.335	22.548	28.373	2.781
1975.....	29.754	4.071	33.825	36.768	3.603
1978.....	6.704	4.184	10.888	13.306	1.304
1979.....	6.546	9.124	15.670	17.580	1.723

[1] in tons, calculated from annual larvae abundance ([spawner biomass = $9.8 \times 10^{-8} \times$ larvae abundance] from Smith 1972).

[2] taken from Appendix I, Table 2, Fishery Management Plan.

BIOMASS ESTIMATE

Anchovy spawning biomass estimates for previous years are based on annual larva abundance estimates. For years in which surveys are conducted in only the winter and spring quarters, the annual larva abundance (L) can be predicted from the winter-plus-spring quarters larva abundance using the regression equation (see Figure 4)

$$L = 1.8233 \times 10^{12} + 1.0055\, L_{WS}\, ;\ R^2 = 0.990 \qquad (4)$$

This equation is slightly different from the one Stauffer and Parker (1980) used for making the 1978 biomass estimate because the historical time series of L_{WS} was recalculated for the redefined regions and with data from only the standard stations. Also, equation (4) was fit to data points for only those years (1951-60, 1966, and 1969) in which surveys were conducted in each half of the winter and spring quarters (see Figure 5).

The 1979 estimate of annual larva abundance using equation (4) is 17.580×10^{12} larvae, where $L_{WS} = 15.670 \times 10^{12}$ larvae. The estimate of the 1979 spawning biomass, B, using Smith's (1972) method,

$$B = 9.8 \times 10^{-8}\, L,$$

is 1,723,000 short tons. This is a 23% increase over the 1978 biomass estimate. The historical estimates of anchovy spawning biomass of the central subpopulation are shown in Figure 5.

OPTIMUM YIELD

As specified in the Northern Anchovy FMP (PFMC 1978), optimum yield for 1979-80 season for the central subpopulation with the estimated spawning biomass of 1,723,000 short tons was 241,000 short tons. Of this amount, the optimum yield in the U.S. zone was 70% or 168,700 short tons. A total of 12,600 tons was reserved for U.S. nonreduction fishing. The 1979-80 reduction quota was 156,100 short tons, of which 10,000 tons were reserved for the fishery north of Point Buchon and 146,100 short tons were available for the U.S. fishery south of Point Buchon.

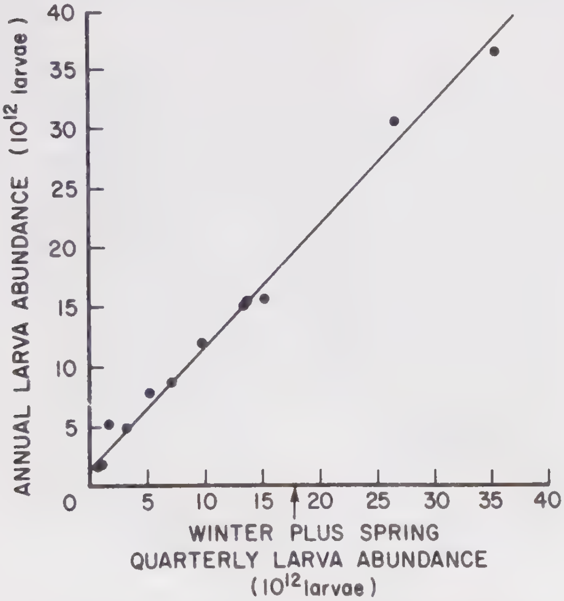

Figure 4. Regression model for estimating the annual larva abundance from winter-plus-spring quarterly larva abundance; arrow indicates 1979 value.

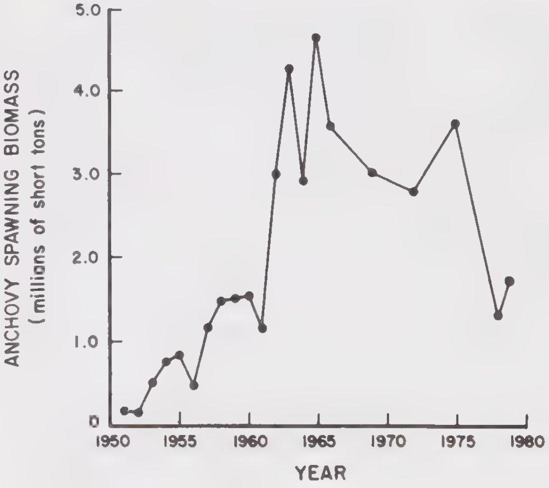

Figure 5. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951-1979.

ACKNOWLEDGMENTS

The collection and processing of the ichthyoplankton data for this biomass estimate depends on the cooperation and hard work of a number of dedicated employees on the staff of the National Marine Fisheries Service (NMFS), Scripps Institution of Oceanography (SIO), and the NOAA ship R/V *David Starr Jordan*. I specifically thank the SIO plankton sorting group, Messrs. James Thrailkill, Richard Charter, Oden Burris, Robert Counts, and William Flerx of NMFS. I thank Drs. Daniel Huppert and Paul Smith of NMFS and Mr. Alec MacCall of California Department of Fish and Game for their useful suggestions and constructive review of this manuscript.

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Stauffer, G.D., and K.R. Parker. 1978. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1978-79 fishing season Calif. Coop. Oceanic Fish. Invest. Rep. 21: (this volume).

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ABSTRACT

The 1978 spawning biomass estimate for the central subpopulation of northern anchovies was 1,304,000 short tons. This estimate is based on the anchovy larva abundance as measured by four egg and larva surveys conducted over the period January-June 1978. Spawning biomass was estimated from larva abundance using Smith's (1972) method. Based on the Pacific Fishery Management Council's Anchovy Plan (PFMC 1978), optimum yield for the central subpopulation during the 1978-79 season was 101,333 short tons. The optimum yield in the U.S. Fishery Conservation Zone was 70,993 short tons. The 1978-79 U.S. reduction quota was 58,333 short tons.

RESUMEN

En 1978 el cálculo de la biomasa del desove para la subpoblación central de anchoveta del norte fue de 1,183,000 toneladas métricas (1,304,000 toneladas). Este cálculo se basa en la abundancia de larvas de anchoveta que se midió en cuatro cruceros de reconocimiento de huevecillos y larvas efectuados en el período enero-junio de 1978. El cálculo de la biomasa del desove se hizo de la abundancia de larvas usando el método de Smith (1972). Basado en el plan de anchoveta del Pacific Fishery Management Council (PFMC 1978), el rendimiento óptimo de la subpoblación central durante la temporada de 1978-79 due de 91,927 toneladas métricas (101,333 toneladas). El rendimiento óptimo en la zona de conservación de la pesquería de los EE.UU. fue de 64,403 toneladas métricas (70,993 toneladas). La reducción de la cuota efectuada por los EE. UU. en 1978-79 fue de 52,919 toneladas métricas (58,333 toneladas).

INTRODUCTION

The Fishery Management Plan (FMP) for the Northern Anchovy Fishery (Pacific Fishery Management Council 1978) requires that catch quotas be determined on the basis of current estimates of spawner biomass. The purpose of this paper is to document the 1978 estimate of spawning biomass of the central subpopulation of northern anchovy from which the optimum yield for the 1978-79 U.S. fishing season was established. The estimate was based on the 1978 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey for the winter and spring quarters. This survey was conducted under the auspices of the La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service. Scripps Institution of Oceanography (SIO), and Instituto Nacional de Pesca (INP), Mexico, cooperated in conducting this survey.

The procedure for estimating anchovy spawning biomass from anchovy larva abundance was based on the method given by Smith (1972), as documented in Appendix I of the FMP (PFMC 1978). In addition, the larva abundance estimate for the 1978 winter and spring quarters was expanded to an annual larva abundance based on the analysis of the historical data.

LARVA SURVEY

The data set of plankton samples for making the biomass estimate included only the four winter and spring surveys out of the eight planned for the 1978 CalCOFI triennial survey year. Only standard CalCOFI stations within the range of the central subpopulation were included even though stations were occupied as far south as CalCOFI line 137 at 25°N and approximately 400 nautical miles offshore on lines 90 and 93 (Figure 1).

Research vessels departed the weeks of 1 January 1978, 12 February 1978, 26 March 1978, and 7 May 1978. Each cruise was approximately 25 days long. The Mexican vessel, R/V *Humboldt*, sampled the southern waters, essentially south of the U.S.-Mexico border; the U.S. vessel, R/V *Jordan*, sampled the waters north of the border. Because of mechanical problems the *Jordan*'s station pattern for the third survey was modified to include the southern stations. The outermost stations within the geographic range of the central subpopulation were dropped from the pattern.

Plankton samples were taken with a CalCOFI Bongo net, a pair of plankton nets with a combined cross-sectional area equal to a CalCOFI 1-m ring net. Plankton data and samples were brought back to the Southwest Fisheries Center (SWFC) for processing and sorting. One-hundred percent of the plankton samples were sorted if the station was beyond 200 miles or if the plankton volume was less than 26 ml; otherwise, a 25% aliquot of the sample was sorted. The only samples sorted for this estimate are from the 118 standard stations defined by Smith (1972) to be those stations routinely occupied since 1951 and within the range of the central subpopulation. These last two criteria were

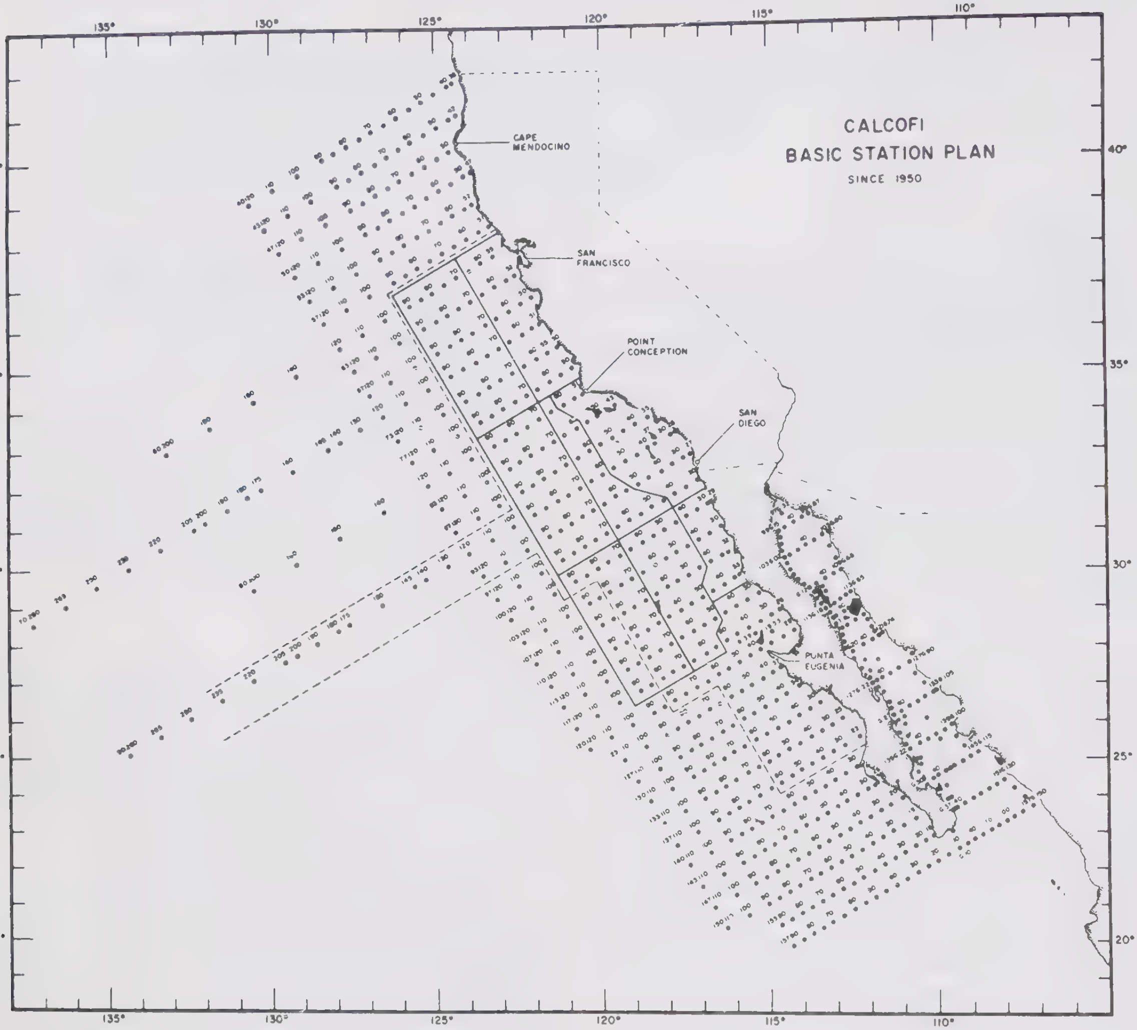

Figure 1. CalCOFI basic station plan. Solid outline is the area of the central subpopulation of northern anchovies. Dashed outline is boundary of winter and spring surveys, 1978.

necessary so that samples could be sorted by the deadline of July 1 for the biomass estimate.

SURVEY RESULTS

The distributions of larvae for the four cruises beginning with the January cruise, which form the basis for the 1978 spawning biomass estimate, are summarized in Figure 2. In general, the spawning intensity in the Southern California Bight and nearshore region was approximately the same as in earlier years, but only about ⅓ of the range of the central subpopulation contained anchovy eggs and larvae. Spawning was most intense during the March cruise. By the May cruise, spawning had fallen off considerably. Ocean temperatures in the upper mixed layer and sea surface from mid-December to mid-April were the warmest since 1958 (J. Renner, SWFC, personal communication). The unusual weather pattern that developed in the latter half of December brought numerous Pacific storms into southern California. These events resulted in increased ocean surface temperatures along the entire U.S. west coast at a time when seasonal cooling normally takes place. The storm activity also at times inhibited the southerly flow of the California Current (Miller 1978). The February or March upwelling did not develop as usual (A. Bakun, SWFC/PEG, personal communication), These conditions may have accounted

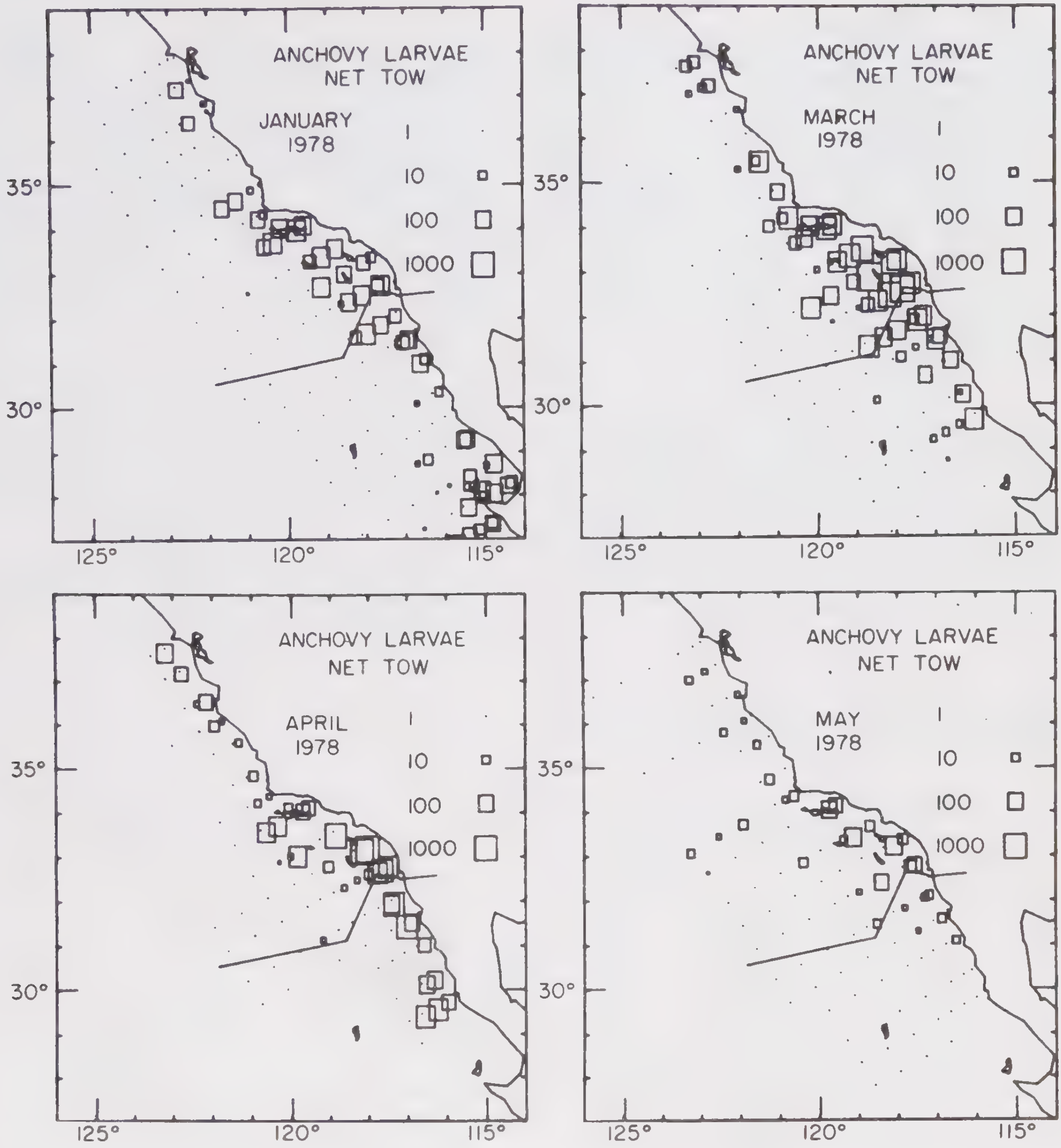
ANCHOVY LARVAE
NET TOW
JANUARY
1978
MARCH
1978
APRIL
1978
MAY
1978
1
10
100
1000
35°
30°
125°
120°
115°

Figure 2. Geographic distribution of anchovy larvae for central subpopulation in winter and spring months of 1978 spawning season. The legend is in numbers of larvae per 10m^2 of surface area.

for the lack of offshore anchovy spawning during winter and spring months.

In the winter quarter, 240 standard stations were occupied and 98 contained anchovy larvae. In the spring, 195 stations were occupied and 64 contained larvae. The number of occupied stations decreased in the spring quarter because the station pattern of the April *Jordan* cruise was modified mid-cruise so that priority stations south of the U.S.-Mexico border would be sampled.

The larva abundance estimates compiled by region quarter strata after Smith (1972) are 6704.1×10^9 and 4183.6×10^9 larvae for the winter and spring quarters, respectively. These give a combined winter-spring larva abundance of $10{,}887 \times 10^9$ larvae.

BIOMASS ESTIMATE

Anchovy spawning biomass estimates for previous years are based on annual larva abundance estimates. Because over 80% of the anchovy spawning takes place in the winter-spring months, the 1978 annual larva abundance ($\hat{L}$) is predicted from the sum of the winter and spring quarters larva abundance (L_{WS}) using the regression equation

$$\hat{L} = 1.062\, L_{WS} + 1743.0 \times 10^9. \qquad (1)$$

This equation is derived from the historical time series presented in Table 2 of Appendix I in the FMP (PFMC 1978) and is repeated here in Table 1. This regression is illustrated in Figure 3. The 1978 estimate of annual larva abundance using (1) is $13{,}305.8 \times 10^9$ larvae, where $L_{WS} = 10{,}887.7 \times 10^9$ larvae. The estimate of 1978 spawning biomass B, using Smith's (1972) method

$$B = 9.8 \times 10^{-8}\, \hat{L} \qquad (2)$$

is 1,304,000 short tons. Historical estimates of anchovy spawning biomass of the central subpopulation are shown in Figure 4.

TABLE 1

Estimated Larva Abundance (10^{12} Larvae) and the Spawner Biomass[1] for the Central Subpopulation[2]

Year	Winter	Spring	Winter and spring	Annual	Spawner biomass in millions of short tons
1951	.298	.690	.988	1.841	.180
1952	.407	.457	.864	1.600	.156
1953	1.210	.373	1.583	5.208	.510
1954	4.469	.988	5.457	7.838	.768
1955	5.588	1.709	7.297	8.618	.845
1956	1.911	1.206	3.117	4.944	.485
1957	5.954	4.308	10.262	11.906	1.167
1958	8.114	5.236	13.350	15.087	1.479
1959	6.341	8.155	14.496	15.440	1.514
1960	7.552	7.547	15.099	15.713	1.540
1961	.992	6.714	7.706	11.827	1.159
1962	4.814	23.567	28.381	30.478	2.986
1963	17,277	24.818	42.195	43.407	4.254
1964	8.941	14.383	23.324	29.599	2.901
1965	19.155	22.690	41.845	47.540	4.650
1966	15.103	15.865	30.968	36.452	3.572
1969	19.756	6.538	26.294	30.594	2.998
1972	8.213	14.335	22.548	28.373	2.781
1975	29.754	4.071	33.825	36.768	3.603
1978	6.704	4.184	10.888	13.306	1.304

[1] in tons, calculated from annual larvae abundance ([spawner biomass = $9.8 \times 10^{-8} \times$ larvae abundance] from Smith 1972).

[2] taken from Appendix I, Table 2, Fishery Management Plan.

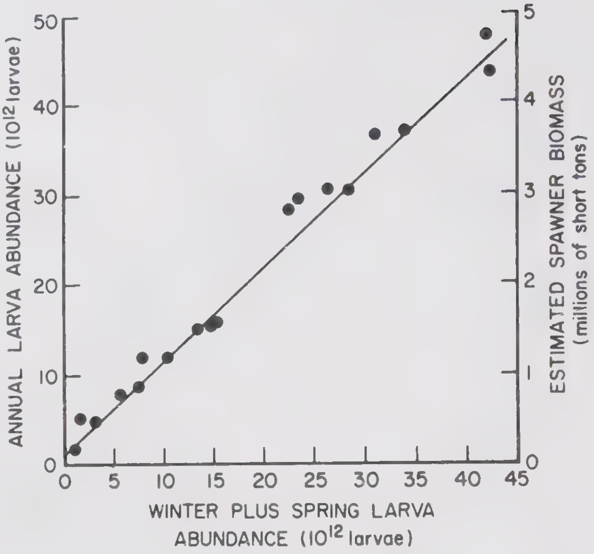

Figure 3. Larva abundance estimates (10^{12} larvae) and estimated spawner biomass in millions of tons. Plot of estimated spawner biomass and annual larva abundance versus winter plus spring larva abundance. Linear regression, Model: $Y = 1.062\, X + 1.743 \times 10^{12}$

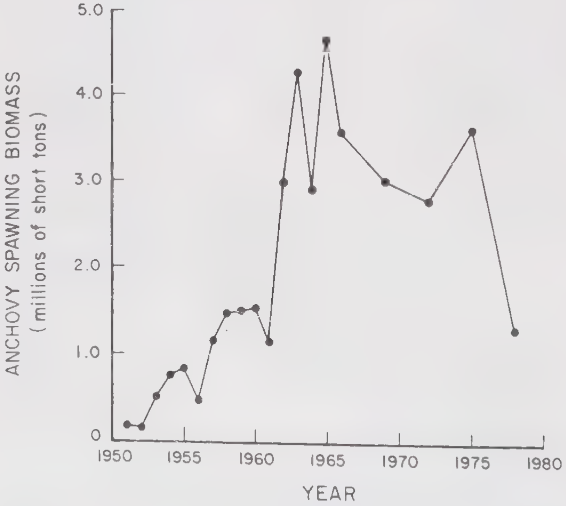

Figure 4. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951-78.

OPTIMUM YIELD

As specified in the Northern Anchovy Fishery Management Plan, optimum yield for the 1978-79 season for the central subpopulation with the estimated spawning biomass of 1,304,000 short tons was 101,333 short tons. Of this amount, the optimum yield in U.S. zone was 70% or 70,933 short tons. A total of 12,600 tons was reserved for U.S. nonreduction fishing. The 1978-79 reduction quota was 58,333 short tons, of which 5,833 tons were reserved for the fishery north of Point Buchon and 52,500 short tons were available for the U.S. fishery south of Point Buchon.

ACKNOWLEDGMENTS

The collection and processing of the ichthyoplankton data for this biomass estimate depends on the cooperation and hard work of a number of dedicated employees on the staff of National Marine Fisheries Service (NMFS), Scripps Institution of Oceanography (SIO), Instituto Nacional de Pesca (INP), and the NOAA ship R/V *David Starr Jordan*. We specifically thank the SIO plankton sorting group, Messrs. James Thrailkill, Richard Charter, Oden Burris, Robert Counts, and William Flerx of NMFS and Mrs. Dorothy Roll of NMFS. We thank Drs. Daniel Huppert and Paul Smith of NMFS and Mr. Alec MacCall of California Department of Fish and Game for their useful suggestions and constructive review of the manuscript.

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8081

Preliminary Investigations of the Possible Relationship Between Passive Behavior by Spotted Dolphins, *Stenella attenuata* and Capture Stress

FINAL REPORT TO THE MARINE MAMMAL COMMISSION
CONTRACT #MMC7AC027
by
Warren E. Stuntz

INTRODUCTION

During the cruise of the tuna purse seiner *Elizabeth C. J.*, behavioral observations were made of porpoise in the purse seine (Norris, Stuntz and Rogers, 1978). One unusual behavior pattern that was observed in the purse seine was labeled "passive behavior." Porpoises showing passive behavior are observed to lie on the bottom of the net and to move awkwardly. In searching for a possible reason for passive behavior, one possibility that suggests itself is a syndrome now being called capture stress or capture myopathy.

"Capture myopathy (CM)" is a syndrome caused by severe exercise or muscular tension brought about by stress. CM was first described in Hunter's antelope (*Damaliscus hunteri*), by Jarrett, et al. (1964) and was called muscular dystrophy. These authors examined and described the pathology of antelope that had died during capture. Since that time, the syndrome has been recognized in a wide range of species including mammals, birds, and fishes (Chalmers and Barrett, 1977; Harthoorn, 1973).

Conditions Causing CM

The conditions under which CM occurs are varied but always involve at least a short period of severe stress. Most common is a chase and subsequent capture such as occur in capturing animals for zoos, research, etc. Transporting animals seems to be especially stressful and CM caused by transport is described by Lewis, et al. (1977) for elk (*Cervus canadensis*) and by Chalmers and Barrett (1977) for pronghorns (*Antilocapra americana*). CM-like symptoms are also seen in domestic animals after transportation and is often called shipping disease.

No cases of CM have been positively diagnosed in a marine mammal. Colgrove (1978) reported on a suspected case of myopathy in a *Tursiops truncatus* that had been transported.

Walker (1975) describes the responses of *Delphinus delphis* in an "advanced state of shock" upon being placed in a tank after capture. Their swimming was "erratic", with "low amplitude tail beats." A behavior pattern where an animal sank to the bottom of the tank was often observed. Mortality was high (75 percent within the first 2 months of captivity). Other species had lower mortality rates, however, the mortality was still high. *Lagenorhynchus obliquidens*, for example, had 50 percent mortality within 6 months of capture; *T. truncatus* had only a 33 percent mortality within the first year of captivity.

Implications for Tuna-Porpoise Situation

Similarities between the capture of porpoises in the eastern tropical Pacific (ETP) purse-seine fishery (see Norris, et al., 1978 for description of purse-seining) and the capture of terrestrial mammals leads to the possibility that CM could be a problem for porpoises. If capture myopathy is occurring, the actual mortality due to fishing is probably substantially higher than is presently estimated.

To date there are no data available indicating that CM occurs in the porpoises taken during purse-seining operations. There are, however, some behavioral patterns that could be associated with CM. The most dramatic of these is passive behavior. In passive behavior porpoises are observed lying on the bottom of the purse seine during the backdown period. These animals simply lie against the webbing, often on their backs until they aparently need to breathe, at which time they come to the surface. Their movements are awkward and stilted. Other animals show what may be a related behavior called "rafting" where they simply lie at the surface and move about very little. If rafting and/or passive behavior are symptoms of CM the problem is serious and widespread. Fortunately, there are other possible explanations for passive behavior and rafting (Norris, et al., 1978) but there are as yet no experimental data available upon which to choose among the various possibilities.

With these considerations in mind, attempts were made to gather some preliminary data on whether or not CM might be a problem in the ETP yellowfin tuna purse seine fishery. This work was done aboard a purse-seiner, the _Margaret L._ under charter to NMFS for studies related to the gear used in the yellowfin tuna purse seine fishery. (See Methods section below.)

My goals were as follow.

1. Conduct in-water observations and experiments to determine if the observed passive behavior of porpoises in tuna purse seines is a manifestation of physiological or psychological stress;
2. As possible, collect blood samples from animals exhibiting various kinds of in-net behavior and have them analyzed to determine if passive animals have abnormal blood chemistries; and
3. Assist NMFS investigators in the preliminary evaluation of techniques and equipment designed to effect the release of porpoise from a purse seine prior to backdown.

The plan for the in-water observations and experiments was to skin dive in the purse seine and locate passive porpoises during backdown. The plan was to touch the passive animals and gauge their responsiveness to handling relative to animals that were not displaying passive behavior. This effort was abandoned due to the depth and chaotic conditions encountered during backdown. Such a plan might be feasible using SCUBA. The same restraints were involved in selectively capturing animals for blood sampling and we finally decided, after several abortive attempts at selectivity, to simply sample blood from as many porpoises as possible.

In addition to the passive behavior study, NMFS personnel were to conduct gear and behavioral experiments to reduce incidental porpoise mortality in commercial tuna seining operations. Specifically, to study the overall dynamics of the backdown channel and the behavior of porpoise and tuna in relation to modifications of the net in the backdown apex. They were also to continue "rollup" prevention experiments initiated aboard the vessel in May 1977.

During the course of this trip, we encountered generally poor fishing conditions and as a result we made only 18 purse seine sets on porpoises. The very small number of sets and the number of experiments to be carried out, greatly limited the amount of work that could be accomplished.

METHODS

The cruise was conducted in the period of 27 October 1977 to 22 December 1977 aboard the NOAA chartered tuna purse seiner M/V Margaret L., Harvey Wells, Master; Richard Williams, Fish Captain. NMFS Cruise #328, NMFS contract number 03-8-M02-18. The vessel is 262 feet long with a 45-foot beam and a draft of 20 feet, 3 inches. She has a fish-carrying capacity of 2,200 tons. Fishing methods employed are described in Norris et al. (1978).

Porpoises were captured by the 3 scientists aboard the Margaret L. by using rubber rafts in the backdown channel. Up to 3 animals could be captured during a single backdown. A large raft and occupant were stationed on the bow side of the backdown channel at the corkline. As porpoises were backed out, the raft was moved closer to the apex for the taking of live porpoise. With the aid of the raftman (or men) in the small inflatable Avon raft (or rafts) the desired number of porpoises were detained at the end of porpoise rescue. Upon capture a porpoise was placed in a rubber raft. When each raft had a porpoise in it, we would tie the 3 rafts together, detach ourselves from the net and drift while taking the blood samples. The animals in the raft(s) were kept wet by one of us. The other two scientists cooperated in restraining the animal in the large raft and in drawing blood.

Blood was drawn from the underside of the flukes in the large visible vein present there. Depending on our qualitative assessment of the animal's condition, 0 ml - 30 ml of blood were taken before the animal was released.

When sampling was complete the samples were returned to the ship and centrifuged to harvest the serum. Hemolysis was a problem and nearly all of the serum samples were affected to some extent. The serum was then frozen and maintained in the frozen state until it was analyzed. The serum was analyzed by a commercial laboratory using a SMAC (serum multiple analysis computer). The excess serum was refrozen and then analyzed later for creatinine phosphokinase (CPK), Lactate dehydrogenase (LDH), and their enzymes. (See Table 1 for constituents analyzed.)

The technique for sampling blood from dead animals was different only in that the blood was drawn directly from the heart. With that exception, the samples were treated like those taken from living porpoises.

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RESULTS

During the cruise, 38 sets were made, of which 18 were on porpoises. A total of approximately 7,345 porpoises were captured along with 172 tons of yellowfin tuna. The 20 non-porpoise sets resulted in 1 ton of yellowfin tuna and 64 tons of skipjack. Porpoise mortality occurred during six sets. Sixteen porpoises were killed during these six sets with mortality rates of 0.89 porpoise per set, and 0.093 porpoise per ton of yellowfin tuna.

During the first 6 sets on porpoises a modification to the backdown channel was tested. The results were unsatisfactory and the system was removed. During two porpoise sets we used dry ice to create a bubble "screen" or "curtain." Due to continual poor weather and current conditions we were unable to make any of the planned prolonged sets.

Blood samples were collected from 15 porpoises. One animal (No. WES 006) (see Table 1) died while blood was being collected and was resampled after death using the sampling techniques for dead animals. A total of 16 samples was taken (the container for one sample broke and was discarded; the data from this porpoise are not included).

In those cases where multiple samples were collected (up to 3, 10 ml samples), each sample was analyzed separately by the SMAC. The results showed very little variation in values between samples and the values for each animal were, therefore, averaged (Table 1).

DISCUSSIONS AND RECOMMENDATIONS

Due to the small sample size no conclusions can be drawn. No significant relationships were found between the chase duration (mean 33.8 min, standard deviation 16.45 min, range 12-61 min) and levels of the various serum constituents nor was the duration of a set (mean 97 min, standard deviation 37.45 min, range 70-172 min) found to be significantly related to the serum constituents

The most important result of this work was a clearer understanding of the difficulties to be encountered in attempting to collect data on CM. Since this first step, a research plan has been developed and is now being implemented by the National Marine Fisheries Service.

The first step of that plan was to convene a workshop on the subject of capture stress. The workshop was held in May 1979 (Stuntz and Shay, 1979).

Table 1. Serum Constituents of Porpoises Sampled.

Sample Number	Position	Sex	Age	LDH* Total V/l	Total Protein g/dl	Globulin g/dl	Albumin g/dl	Inorganic Phosphates mg/dl	Creatinine Phosphokinase(CAK) v/l
Living									
WES 001	30°7'N 110°35'W	Unknown	Two-toned	Off scale	5.8	1.50	4.3	7.2	186
WES 002	31°13'N 110°8'W	Female	Mottled	Off scale	6.6	2.50	4.1	5.0	130
WES 003	"	Female	Mottled	Off scale	6.2	2.45	3.7	5.6	67
WES 006	3°51'N 106°3'W	Female	Speckled	Off scale	6.6	2.50	4.0	5.8	70
WES 007	4°14'N 102°36'W	Male	Adult	Off scale	6.6	2.00	4.6	5.0	28
WES 011	6°8'N 93°42'W	Female	Adult	Off scale	7.8	3.47	4.3	3.8	60
WES 012	"	Female	Adult	Off scale	7.0	2.63	4.3	5.1	18
WES 013	"	Male	Mottled	Off scale	5.3	1.43	3.9	4.4	74
WES 014	7°29'N 85°43'W	Male	Adult	Off scale	6.9	2.43	4.3	6.0	42
WES 015	"	Male	Adult	62.0	7.2	3.10	3.7	4.9	9
Dead									
WAS 006	3°51'N 106°31W	Female	Speckled	Missing	7.4	2.63	4.8	Missing	111
WES 004	3°13'N 111°8'W	Male	Adult	Missing	7.3	3.05	4.2	7.4	149
WES 005	"	Female	Mottled	Missing	8.5	3.20	5.3	9.2	339
WES 008	4°14'N 102°36'W	Female	Speckled	Missing	8.0	3.23	4.7	9.4	74
WES 010	"	Male	Neonate	Missing	4.9	Missing	5.4	Missing	3099

* Lactate dehydrogenase

Table 1. Continued

Sample Number	Sex	Age	Bun/ Creatinine	Cholesterol mg/dl	Total Bilirubin mg/dl	SGPT* U/L	Alkaline phosphatase U/L	SGOT** U/L	Serum Iron mg/dl	Triglycerides mg/dl
Living										
WES 001	Unknown	Two-toned.	39.33	170	.2	64	missing	282	163	71
WES 002	Female	Mottled	51.43	165	.3	84	403	330	145	99
WES 003	Female	Mottled	46.47	172	.2	37	212	224	180	60
WES 006	Femalé	Speckled	42.00	165	.4	36	436	222	122	51
WES 007	Male	Adult	43.96	248	.4	missing	138	missing	174	78
WES 011	Female	Adult	58.30	158	.4	59	154	259	175	200
WES 012	Female	Adult	54.81	218	.1	33	192	237	126	113
WES 013	Male	Mottled	59.17	166	.2	71	431	254	133	185
WES 014	Male	Adult	50.08	181	.1	76	252	239	158	152
WES 015	Male	Adult	65.56	312	.1	74	100	232	208	230
Dead										
WAS 006	Female	Speckled	36.11	196	0.4	57	488	365	244	54
WES 004	Male	Adult	45.21	181	0.2	75	203	292	180	80
WES 005	Female	Mottled	49.33	[illegible]	[illegible]	[illegible]	23	365	0	178
WES 008	Female	Speckled	48.07	168	0.3	121	500	Missing	182	75
WES 010	Male	Neonate	45.00	260	0.3	Missing	Missing	121	501	438

* Serum Glutamic pyruvate transaminase
** Serum Glutamic oxaloaretic transaminase

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Table 1. Continued

Sample Number	Sex	Age	Creatinine Phosphokinase isoenzymes		Lactate dehydrogenase isoenzymes				
			CPK_1 U/L	CPK_2 U/L	LDH_1%	LDH_2%	LDH_3%	LDH_4%	LDH_5%
Living									
WES 001	Unknown	Two-toned	115	71	5	17	38	26	14
WES 002	Female	Mottled	90	40	7	18	34	27	14
WES 003	Female	Mottled	40	27	6	18	34	27	15
WES 006	Female	Speckled	50	20	15	15	32	25	13
WES 007	Male	Adult	21	7	4	18	36	30	12
WES 011	Female	Adult	10	50	8	17	35	27	13
WES 012	Female	Adult	10	8	9	11	37	26	17
WES 013	Male	Mottled	30	44	10	15	32	26	17
WES 014	Male	Adult	15	27	8	18	33	26	15
WES 015	Male	Adult	9	0	8	17	33	30	12
Dead									
WAS 006	Female	Speckled	90	21	10	24	32	21	13
WES 004	Male	Adult	100	49	6	17	37	26	14
WES 005	Female	Mottled	150	189	8	17	34	26	12
WES 008	Female	Speckled	60	14	10	22	34	22	12
WES 010	Male	Neonate	1850	1249	24	25	23	17	11

Table 1. Continued

Sample Number	Sex	Age	Glucose mg/dl	Creatinine mg/dl	Urea Nitrogen mg/dl	Uric Acid mg/dl	Sodium mg/dl	Chloride mg/dl	Potassium mg/dl	Calcium mg/dl
Living										
WES 001	Unk	Two-toned	178	1.5	59	1.1	157	119	6.6	6.1
WES 002	Female	Mottled	164	1.4	72	1.2	152	116	5.2	7.9
WES 003	Female	Mottled	154	1.7	79	.8	150	119	4.1	8.7
WES 006	Female	Speckled	122	1.5	63	1.2	156	118	4.9	9.3
WES 007	Male	Adult	100	1.6	68	.7	141	111	6.3	8.3
WES 011	Female	Adult	134	1.2	68	.7	153	118	4.6	8.6
WES 012	Female	Adult	120	1.3	73	1.7	missing	114	5.0	10.1
WES 013	Male	Mottled	122	1.2	71	.8	154	123	5.2	8.0
WES 014	Male	Adult	111	1.3	62	1.5	150	118	5.6	8.3
WES 015	Male	Adult	87	1.0	64	1.5	136	116	6.0	7.1
Dead										
WAS 006	Female	Speckled	117	1.8	65	2.2	157	113	Missing	11.3
WES 004	Male	Adult	213	1.6	74	1.5	158	120	10	10.8
WES 005	Female	Mottled	234	1.5	74	2.8	Missing	119	Missing	0.0
WES 008	Female	Speckled	Missing	1.7	79	3.0	158	117	Missing	12.9
WES 010	Male	Neonate	145	1.6	72	1.1	152	112	Missing	14.5

The workshop concluded that capture stress was probably causing some mortality in porpoises involved in the ETP tuna fishery. The workshop also addressed the problem of how to collect data on the level of stress in dolphins. The major conclusion was that an experiment should be done on *Delphinus delphis*, the common dolphin, in waters near San Diego, CA. The study would be designed to determine (1) if capture stress occurs in dolphins, and (2) if so, what the best techniques are for measuring the stress levels.

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8082

FOOD AND FEEDING OF PACIFIC HAKE LARVAE, *MERLUCCIUS PRODUCTUS*, OFF SOUTHERN CALIFORNIA AND NORTHERN BAJA CALIFORNIA

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ABSTRACT

The diet of larval Pacific hake, *Merluccius productus*, consisted primarily of copepod eggs and calanoid copepod adults, copepodites, and nauplii, based on an examination of material collected in March 1975 off southern California and northern Baja California. In spite of a large mouth, Pacific hake larvae ingested a broad size range of prey, with a concentration of food particles 70-200 μm in width. First-feeding Pacific hake larvae fed upon a wide range of prey (50 to about 400 μm prey width), and the range in prey sizes changed little with larval length from 3.0-10.7 mm. Although copepod eggs, nauplii, and copepodites were a significant portion of the diet in numbers of prey, adult copepods contributed about 74% of prey volume.

Observations of feeding incidence in relation to time of capture revealed a slow rate of gut evacuation. Larvae began feeding at about 1000 hours, and the number of prey items found in the gut increased during the day, reached a maximum after sunset, and thereafter decreased gradually. The comparatively large mouth, slow evacuation rate, and ability to feed on copepod stages from egg to adult seem to form an adaptive strategy for success in the relatively deep and cold strata inhabited by Pacific hake larvae.

RESUMEN

El examen del material colectado en marzo de 1975 en las costas del sur de California y del norte de Baja California indicaría que la dieta de las larvas de merluza del Pacífico, *Merluccius productus*, consiste principalmente de huevecillos de copépodos y adultos copépodos calanoides, copepoditos, y nauplios. Las larvas de merluza del Pacífico, a pesar de tener una boca muy grande, ingirieron presas de muy variados tamaños, con una concentración de partículas de comida que alcanzaba de 70-200μm de anchura. Las larvas de merluza del Pacífico se alimentaban primero de una amplia calidad de presas (de 50 a 400μm anchura de presa), y la amplitud de tamaños de presas cambió poco con las larvas de longitudes de entre 3.0 a 10.7 mm. Aunque los huevecillos de copépodos, nauplios, y copepoditos formaron una parte significativa de la dieta en cuanto a su frecuencia como presa, los copépodos adultos formaron aproximadamente 74% del volumen de la presa.

Observaciones sobre las incidencias del alimento en relación con el tiempo de captura presentaron una proporción muy baja de evacuaciones intestinales. Las larvas empezaron a comer alrededor de las 1000 horas, y el número de presas encontradas en el intestino aumentó durante el día, alcanzando un máximo después de la puesta del sol, y disminuyendo después gradualmente. La boca comparativamente grande, una baja proporción de evacuaciones, y la habilidad de alimentarse de todas las fases de desarrollo de los copépodos, desde huevecillo hasta adulto, forman conjuntamente una estrategia de adaptación perfecta al complejo faunístico de los estratos relativamente profundos y fríos habitados por las larvas de merluza del Pacífico.

INTRODUCTION

Pacific hake[1] larvae (*Merluccius productus*) are the second most abundant pelagic fish larvae in the California Current, being surpassed only by larvae of the northern anchovy, *Engraulis mordax* (Ahlstrom 1965; MacGregor 1966). A hake fishery exists off the California-Washington coast, exploited primarily by foreign trawlers (Grinols and Tillman 1970; Pacific Fishery Management Council 1979). Information is available on larval development and distribution and on adult spawning and feeding of *M. productus* (Ahlstrom and Counts 1955; Ahlstrom 1959, 1969; Kramer and Smith 1970; Smith and Richardson 1977; Bailey 1980; Best 1963; Alton and Nelson 1970). In contrast, little is known of the feeding habits of Pacific hake larvae, although studies have been undertaken for larvae of *Merluccius merluccius hubbsi* in the South Atlantic (de Ciechomski and Weiss 1974) and for other kinds of gadoid larvae and juveniles (Marak 1960; Sysoeva and Degtereva 1965; Bainbridge and McKay 1968; Arntz 1974). The present report analyzes data obtained on gut contents, mouth size, and feeding incidence of Pacific hake larvae.

METHODS AND MATERIALS

A total of 298 larvae, 3.0-10.7 mm in length, from 18 formaldehyde-preserved samples taken during the March 1975 CalCOFI cruise aboard the R/V *David Starr Jordan* were examined. Stations represented cover a region 33° 25′ to 29°02′ N by 115°18′ to 120°54.5′ W, roughly off San Pedro, California, to south of Punta Baja, Baja California. All samples were collected with a 505-μm

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[Manuscript received 3 March 1980.]

[1] The common name "pacific hake" has been replaced by "Pacific whiting" for *Merluccius productus* by the marketing and fishing industry, however, the former name is retained in this work.

mesh, 1-m aperture plankton net, towed obliquely from an approximate depth of 210 m to the surface. When samples contained more than 100 hake larvae, subsamples of 25 were randomly selected over a representative size range for dissection.

Body lengths (measured from the tip of the snout to the tip of the notochord) were recorded from the specimen on a glass slide under a stereomicroscope. In order to hold the larva in position for mouth width measurements, a plexiglass plate was etched with a size gradient of grooves, and the larva was placed along its dorsal body edge in the appropriate sized groove with its upper and lower jaws held open at about 90° for the measurement.

The entire gut was removed intact from each specimen and was placed in a drop of glycerin on a glass depression slide (see Arthur 1976). Using probes tipped with pig's eyelashes, the mid- and hindgut walls were carefully slit open, and prey organisms teased out. A drop of lactic acid pigmented with Chlorazol Black E saturated in 70% ethanol was added to the gylcerin to stain crustacean cuticle (Judkins and Fleminger 1972), greatly improving the visibility of the prey and facilitating their enumeration and measurement (maximum width). Identifications of food particles were made to the lowest taxa possible with the aid of a compound microscope.

Food volume index was calculated for each food particle by treating copepod eggs as spheres, and nauplii, copepodites, and adults as ellipsoids. The ellipsoidal length for nauplii was generalized as twice the width, and for copepodites and adults, 2.5 times the width. Thus, the general volumetric equation, $V = 4/3\ \pi abc$, where a, b, and c are diameters along the three axes, could be used to calculate a food volume index for the principal food components. Singular cases of oddly shaped food items, such as fish and polychæte larvae, were measured and treated individually for volume computations.

RESULTS

Composition of Food

Copepod eggs, calanoid adults, copepodites, and nauplii were the principal components of ingested material (Table 1). The copepods *Clausocalanus, Paracalanus, Calocalanus*, and the cyclopoid *Oithona* occurred the most frequently. The rather low diversity of food organisms indicates that hake larvae may feed selectively. This problem could not be investigated because the samples were from oblique integrated tows. No significant variations in the composition of diet were indicated in day versus night or inshore versus offshore samples.

One case of cannibalism (common in adults, Best 1963) occurred, in which two yolk-sac larvae were preyed upon by a 5.5-mm hake larva. The two larvae were partially digested in the midgut of the predator hake larva, providing evidence against the possibility of net feeding.

Size of Food

Pacific hake larvae fed on a wide size range of food particles (Figure 1), ingesting prey almost as large as their maximum mouth width (Figure 2) soon after yolk absorption. Larvae ingested an abundance of copepod eggs, nauplii, and copepodites as well as larger organisms such as adult copepods at larval lengths up to 8 mm (Figure 1). However, examination of the cumulative frequency distribution of numbers and volume of prey types (Table 2) reveals that adult copepods constitute the bulk (ca. 74%) of prey volume, and copepod eggs less than 1%. Of 27 yolk-containing larvae examined, 7 had begun feeding before yolk depletion.

TABLE 1

Food Composition of Pacific Hake Larvae.

	Size range (mm)											
	3.0-3.9		4.0-4.9		5.0-5.9		6.0-6.9		7.0-7.9		8.0-10.9	
Food item	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Copepod adults:												
Clausocalanus spp.	25		51		38		23		8			
Paracalanus spp.	19		39		21		6					
Calocalanus spp.	5		10		17		16		3			
Calanus spp.			1						2			
Mecynocera clausi			6		10		4					
Oithona spp.	2		13		32		10		6		4	
Calanoid-unidentifiable	6		9		14		20		7		1	
Disintegrated	5		7		8		2				3	
Total adults	62	17.7	136	22.0	140	20.4	81	37.3	26	37.7	8	88.9
Copepodites:												
Calanus spp.	1		5		5		5		1			
Oithona spp.	2		13		7		2					
Calanoid (most are *Paracalanus/ Clausocalanus)*	72		84		99		10		4			
Cyclopoid	2		5		6		18		1			
Disintegrated	14		31		15				2			
Total copepodites	91	26.0	138	22.3	132	19.2	35	16.1	8	11.6		
Copepod nauplii:												
Calanoid	102		98		141		39		5			
Cyclopoid	29		20		16							
Disintegrated	1		2									
Total nauplii	132	37.7	120	19.4	157	22.8	39	18.0	5	7.2		
Copepod eggs, single	58		214		251		62		29			
Copepod eggs, clusters	1		5		4							
Total copepod eggs	59	16.8	219	35.4	255	37.1	62	28.6	29	42.0		
Unidentified invertebrate eggs	2	0.6	5	0.8								
Polychæte larva					1	0.1						
Hake yolk-sac larvae					2	0.3						
Mollusc larva											1	11.9
Unidentified crustacean fragment	3	0.9	1	0.2					1	1.4		
Unidentified particles	1	0.3			1			0.1				
TOTAL NUMBER FOOD ITEMS	350		619		688		217		69		9	
Number larvae examined ($\sum$=298)	86		113		72		16		8		3	
Number larvae empty ($\sum$=90)	29[1]		38		18		3		1		1	

[1] 20 with yolk

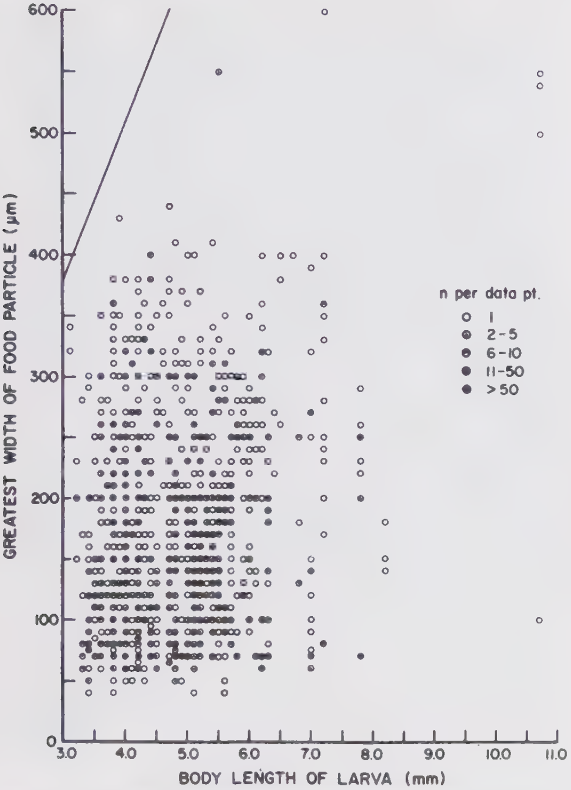

Figure 1. Food size of 208 Pacific hake larvae. Diagonal line indicates maximum mouth width.

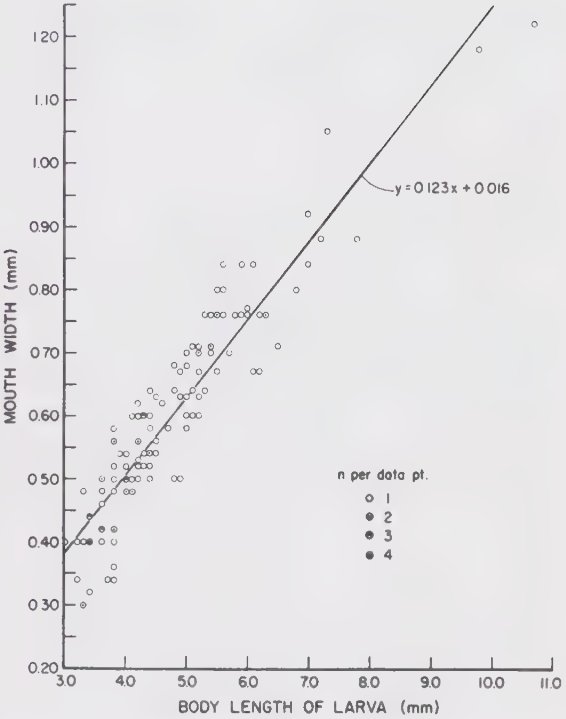

Figure 2. Mouth width of Pacific hake larvae. The correlation with body length is $r = 0{,}93$.

Feeding Incidence

Feeding incidence is defined by Arthur (1976) as the percentage of larvae containing at least one food item in the gut for a given sample. This term refers to presence of food in the gut and does not necessarily reflect recent feeding activity. Analysis of feeding incidence of Pacific hake larvae at time of capture (Figure 3) shows presumptive diurnal feeding activity followed by a slow digestion rate with complete gut evacuation occurring between 0600 and 0800 hours PST. That evacuation rates are slow was supported by the extent of digestion and decomposition of prey organisms in larval hake stomachs; food items from specimens collected between 0400 and 0930 hours showed progressive disintegration over the time range, whereas larvae captured after 1000 hours contained prey in the freshest condition, indicative of first feeding in their diurnal feeding rhythm.

TABLE 2

Cumulative Frequency Distribution of Numbers and Volume for Major Prey Types Found in *M. productus* Larvae.

Prey	Range max. width (μm)	Mean food volume ($10^6\ \mu m^3$)	Standard deviation ($10^6\ \mu m^3$)	Frenquency	Frequency × volume ($10^9\ um^3$)	% of total volume
Copepod eggs	50-100	0.364	0.083	674	0.24534	0.7
Copepod nauplii	40-300	4.013	5.148	441	1.76973	5.3
Copepodites	80-450	14.698	24.308	393	5.77631	17.4
Adult copepods	110-600	57.418	54.850	426	24.46007	73.8
Other	40-550	49.401	107.783	18	0.88922	2.7
					$\Sigma = 33.14067$	

Plots of the mean number of prey and mean food volume index for larvae per sample (Figure 4) are dissimilar in shape. The number curve indicates an increasing accumulation of prey after 1000 hours towards a peak after sunset, whereas the volume index curve is variable and does not show such a trend.

DISCUSSION

Much attention has been given to feeding of marine fish larvae as a factor in larval survival and its effect on population dynamics of fishes. May (1974) and Hunter (1976; in press) provide excellent reviews and discussion of gut content studies in the literature. De Ciechomski and Weiss (1974) showed that hake larvae (*Merluccius merluccius hubbsi*) off Argentina have a very high incidence of feeding (94% during spring) that contrasted sharply with the low feeding incidence (28%) of anchovy (*Engraulis anchoita*) larvae. Feeding incidence is as

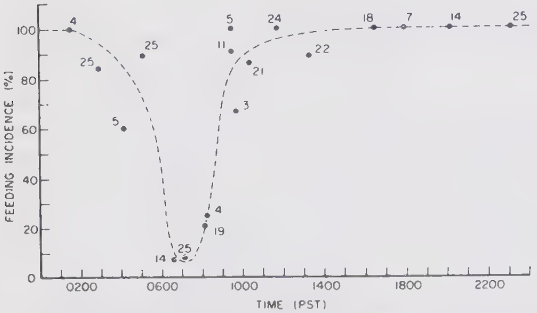

Figure 3. Feeding incidence of Pacific hake larvae in relation to time of capture. Values of data points indicate sample size of larvae. Feeding yolk-sac larvae were excluded from percentage calculations.

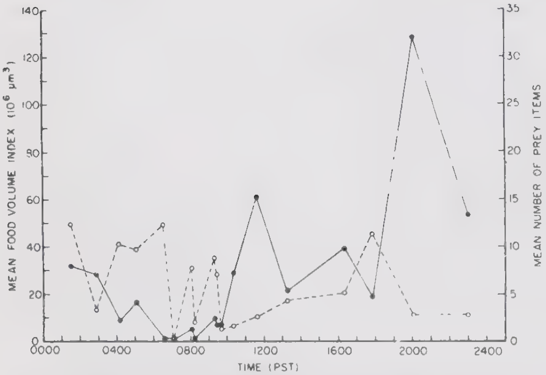

Figure 4. Mean food volume index (dashed line) and mean number of prey (solid line) of hake larvae. Asterisk indicates volume for small sample at 0944 hours when it includes a 7.2-mm hake larva that preyed on a single, unusually large copepod, which was the largest prey encountered in this study.

great or greater for small samples of Pacific hake larvae (up to 100%), but feeding incidence for larvae of the northern anchovy (*Engraulis mordax*) averages less than 10% (Arthur 1976). This disparity in the feeding incidence of two dominant spring ichthyoplankters off California and off Argentina is partly explained by defecation by larvae at time of capture and preservation, especially those with straight guts as found in clupeoid larvae (see Arthur 1976). Hake larvae, however, have folds and a pronounced loop in the gut, which would aid in food retention during capture.

According to de Ciechomski and Weiss (1974), larvae of *M. merluccius hubbsi* feed almost exclusively on copepodites and adult copepods, with calanoids dominating the diet. Average prey width increases from about 500 μm at first feeding to 800 μm at 8-mm larval length. Copepods, particularly calanoids, also dominate the diet of Pacific hake larvae; however, copepod eggs and nauplii constitute about half of the diet items throughout the size range studied (Table 1). Despite their high incidence in the diet, these small-sized prey items contribute only about 6% of the total food volume of prey (Table 2). Hake larvae may be dependent on the successful capture of copepodites and adult copepods to provide the required nutritive level for survival and growth.

First-feeding Pacific hake larvae are capable of feeding on a large size range of prey (50- to about 400-μm prey width), and the propensity to exploit prey organisms throughout this size range persists even in the largest larvae examined in our study. In contrast, clupeoid larvae tend to have relatively small and restricted prey size ranges that are more closely correlated with mouth size (Arthur 1976). Larvae of jack mackerel (*Trachurus symmetricus*) are intermediate between clupeoids and Pacific hake with respect to prey size range. According to Arthur (1976), first-feeding jack mackeral larvae contain prey items in the 50- to 200-μm size range (mostly copepodites and adult copepods). Maximum prey size increases with larval size (to about 400 μm at 7-mm larval length), and larvae tend to exploit prey over a wide size range, although to a lesser extent than do larvae of Pacific hake. Availability of prey organisms is an important factor contributing to prey sizes consumed. Examination of the spawning periods and the distribution and abundance of major prey items in the region would be helpful in understanding these observations on larval feeding.

In *M. productus* larvae, the number of prey items in the gut increases during the day, reaches a maximum after sunset, decreases during the night, and reaches a minimum at dawn (Figure 4). Bainbridge and McKay (1968) showed a similar sequence for cod (*Gadus morhua*) larvae in the north Atlantic, where the number of identifiable copepod nauplii peaked after sunset. Their data for redfish (*Sebastes marinus*) larvae show a pre-sunset peak for number of nauplii in the gut. Arthur (1976) showed a gradual increase in feeding incidence in Pacific sardine (*Sardinops sagax*) during the day, reaching a peak before sunset, followed by a gradual decline during the night. Last (1978) found that the number of prey items of three species of flatfish larvae (plaice, flounder, and sole) reached a peak after sunset, whereas a fourth species, the dab, reached a pre-sunset peak. The disparity between the curves for mean volume and mean number of prey in hake larvae could be due to a longer digestion rate for large prey such as adult copepods, which would be retained in the gut longer and would be reflected in the variable peaks in mean volume despite a low number of prey organisms (Figure 4). The curve for number of prey may then reflect greater temporal sensitivity to feeding activity on smaller prey such as copepod eggs and nauplii.

Since marine fish larvae, including hake, are primarily visual feeders (see review by Hunter, in press), the post-sunset feeding peak shown by hake and some other species is intriguing. One would expect that feeding success would diminish markedly at sunset, providing they do not switch over to another sensory modality at dusk. Initial speculation that hake larvae, unlike most fish larvae, develop rods in their retina early in life, thereby allowing greater visual perception in diminishing light, proved unfounded. A lack of rod development in hake larvae through 8 mm and the formation of rods in a 13.4-mm larva were observed in histological sections of the eye (O'Connell, personal communication). The development of rods in hake larvae between 8 and 13.4 mm indicates that they are similar to anchovy larvae (O'Connell in press), which initiate retinal rod formation at 10-12 mm and which are visual feeders and probably representative of most pelagic fish larvae. Another explanation may be that possible vertical migration of prey after sunset increases the probability of encounters for feeding success. A further possibility is that the general metabolic level of hake larvae declines at sunset, producing a decline in gut evacuation rate and consequently an apparent post-sunset feeding peak. Perhaps the post-sunset feeding peak may result from a combination of these suggested causes.

Adult and juvenile Pacific hake are considered to be opportunistic feeders owing to the variety and availability of their prey organisms (Best 1963; Alton and Nelson 1970). In addition to a host of invertebrates and fish species, adult hake stomachs have contained smaller hake (Best 1963). The propensity to cannibalize is expressed early in ontogeny. The finding of cannibalism by a small hake larva in this study raises the possibility that this could be an important mortality factor when patches of yolk-sac larvae are spatially contemporary with larger larvae and juveniles. If cannibalism is a characteristic of hake larvae, one could speculate that the comparatively short spawning period of this species, late January to late March (Smith and Richardson 1977), enhances survival by reducing size heterogeneity within the larval population and consequently reducing the proportion of potential cannnibals. It would be of interest to investigate further the degree of cannibalism by Pacific hake larvae, whether opportunistic or deliberate, and to determine its role in the ecology and density-dependent dynamics of hake populations.

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8083

Fin Whale and the Dye Marker

From 1974 to 1977 biologists from the University of California, Santa Cruz, under contract for the United States Department of the Interior's Bureau of Land Management, have conducted monthly aerial surveys of whales and dolphins in the Southern California Bight. On the afternoon of 22 January 1977, the authors, Tom Dohl, Project Manager for the survey, and Paul Sund, while flying in a small observation plane off San Clemente Island, sighted a whale about five nautical miles from China Point. The animal was lying motionless on its left side just below the sea surface; and in this position the white baleen and lower lip on the right side of the whale were plainly visible, making possible its positive identification as a fin whale (*Balaenoptera physalus*).

Soon afterward we noticed a disturbance about two miles away. Because the fin whale was not moving, we decided to mark its location with floating fluorescent dye marks, investigate the new activity, and return. We dropped five dye markers in a 300-meter ring around the whale.

We flew back to the area after about four minutes and relocated the fin whale, which was approaching the dye plume extending from one of the markers. As biologists, we immediately considered this behavior noteworthy because it appeared to be an example of the awareness and curiosity of the whale toward unusual objects in the ocean. We observed and photographed this animal for more than twenty-two minutes.

The whale somehow had sensed and located the dye plume, and moved along it from an area of low dye concentration toward the source. The animal's mouth was slightly agape, but we did not observe any perceptible disturbance of the plume and supposed that the whale was not "tasting" the dye. It appeared that the whale most likely was visually keying on the plume from below and within. It had assumed an arcuate position conforming to the shape of the plume and continued to maintain this posture while swimming toward the dye source. This behavior was most noteworthy since it demonstrated the animal's active awareness of the form and boundaries of the plume.

This incident brought to mind a similar event that one of us had observed on 23 January 1973, while flying off Monterey, California, during an aerial photo-system testing exercise. At that time similar dye markers plus smoke flares were dropped from the aircraft to mark the approximate locations of gray whales. On two occasions whales altered their direction to approach and presumably "investigate" the objects.

This observation raises a number of questions that remain to be answered:

How and why did the whale become aware of so small an object as the dye marker (approximately 1″ x 1″ x 3″)?

How did it sense the concentration of the dye; why did it swim into the plume at an area of low concentration and proceed along it toward the source? How did it sense the arcuate form of the plume and why did the whale mimic that shape while swimming along the plume toward the marker?

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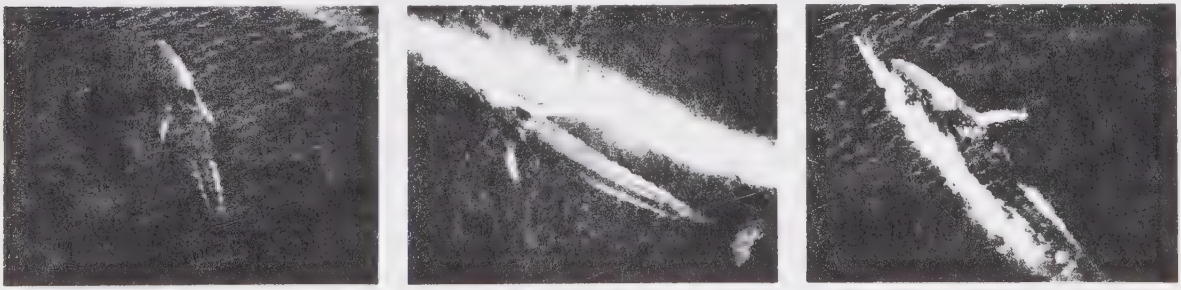

After dropping a dye marker into the water, scientists watched from a research plane as the fin whale (Balaenoptera physalus) *first approached the tail of the dye plume, then took a parallel position to it as it swam toward the source, and finally passed the small globe emitting the dye.*

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CHANGES IN BODY MEASUREMENTS OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND OTHER FISHES DUE TO HANDLING AND PRESERVATION

GAIL H. THEILACKER[1]

ABSTRACT

The relation between northern anchovy length and body parts was compared for live and laboratory-preserved larvae as well as larvae treated in a net to simulate field collection conditions. Larvae were damaged by net abrasion, and those netted before preservation shrank more than those that were laboratory preserved (that is, larvae pipetted directly into preservative). Shrinkage of net-treated individuals decreased with age and increased with handling time, but shrinkage of laboratory-preserved larvae was constant for the size class studied. The results show that morphological differences reported for laboratory-reared and sea-caught larvae of the same length may result from the method of handling larvae prior to preservation.

To describe life stages of larval fish, field and laboratory studies rely on length measurements of preserved sea-collected and preserved laboratory-collected larvae. Sea-collected larvae incur mechanical damage, abrasion from the collecting net and from other plankters, while the net is being towed and washed down (Ahlstrom 1976). When damaged, delicate larvae shrink. This initial shrinkage usually occurs before death, and this shrinkage is compounded by preservative shrinkage (Blaxter 1971). Conversely, laboratory handling of larvae prior to preservation is less damaging than net abrasion. In the laboratory, individual larvae are usually transferred by pipette or beaker to preservative, and they die and shrink in the preservative.

Laboratory-reared fish larvae differ morphologically from sea-caught larvae. Body depth of wild herring, *Clupea harengus*, larvae was smaller than that of starved laboratory-reared larvae of the same preserved length (Blaxter 1971). Ryland (1966) observed that sea-sampled larval plaice, *Pleuronectes platessa*, were smaller than laboratory larvae at a comparable stage and suggested that a factor for shrinkage was needed to equate field with laboratory measurements. I have noticed a similar discrepancy in preserved length of sea-collected yolk-sac larvae and laboratory-hatched and preserved yolk-sac larvae of the jack mackerel, *Trachurus symmetricus* (Theilacker unpubl. data). These morphological differences may be the result of the method of handling (laboratory capture or net capture) prior to preservation. Since it is necessary to compare animals at the same developmental stage to relate laboratory larval fish studies to the field, there is a need to intercalibrate field (preserved) and laboratory (live and preserved) larval fish measurements.

METHODS

Adult northern anchovy, *Engraulis mordax*, maintained in the Southwest Fisheries Center's aquarium, were spawned by hormone injection (Leong 1971). I reared the anchovy larvae at 15.5° C on cultured food organisms (*Gymnodinium splendens*; rotifers, *Brachionus plicatilis*; and copepods, *Tisbe furcata*) in 100 l tanks using methods described by Lasker et al. (1970), Theilacker and McMaster (1971), and Hunter (1976).

I considered several factors that could affect shrinkage of larval fish: 1) size, 2) type of fixative, 3) treatment of larvae before fixation (net or laboratory capture), and 4) duration of net retention. Larval fish measurements fit into four treatment categories (Figure 1): 1) live, 2) laboratory pipetted and preserved, 3) net treated, and 4) preserved after net treatment (equivalent to "field-collected" larvae). Five body measurements (in millimeters) were taken: standard length (SL), tip of upper jaw to perpendicular at end of notochord; head length, tip of upper jaw to cleithrum; body depth at the pectoral (not measured

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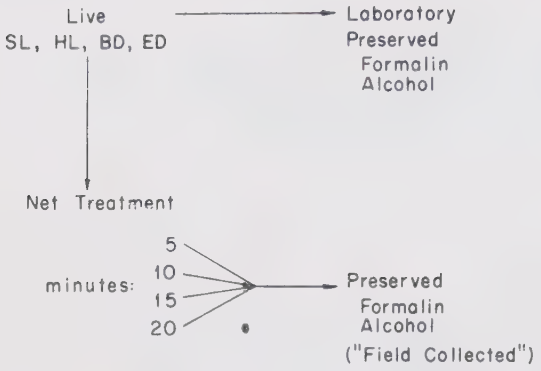

FIGURE 1.—Experimental design. Four measurements of larval northern anchovy were taken to estimate shrinkage during handling treatments: standard length, SL; head length, HL; body depth at the anus, BD; and eye diameter, ED.

for northern anchovy); body depth at the anus; and eye diameter. I kept track of individual larvae during all treatments and determined body part shrinkage on an individual basis. The same larva could be measured as many as six times; e.g., a "field-collected" larva was measured live, after four time intervals in the net, and again after preservation. However, not all net-treated larvae were measured for four time intervals. I used several preservatives: Bouin's fixative, usually used for histological studies; 5% buffered Formalin[2] (2.2% formaldehyde), the standard ichthyoplankton-survey preservative (Ahlstrom 1976; Smith and Richardson 1977); and 80% ethyl alcohol, preservative for otoliths (Methot and Kramer 1979). In treatments (2) and (4), larvae were kept in preservative for 4-5 wk before remeasuring.

As an example of laboratory handling procedures, I have included results from ongoing studies on morphology of jack mackerel and Pacific barracuda, *Sphyraena argentea*, larvae. Eggs of jack mackerel and Pacific barracuda were collected 30-50 km off the coast of southern California in June and July 1977, and rearing procedures were the same as for northern anchovy. Laboratory handling in this study consisted of pipetting live larvae 1) onto a slide for measurement and 2) into preservative. Time spent handling was an important factor affecting shrinkage. Larvae shrink during the measuring process. In this study, all live and laboratory shrinkage measurements include about a 30 s handling time. Some scientists measure laboratory-reared larvae only after preservation; these larvae are probably handled <30 s.

In his paper on the quality of field-collected fish larvae, Ahlstrom (1976) noted several conditions that damaged specimens: fast net speeds, high temperatures, and increased time in the net. During standard ichthyoplankton surveys, larvae in the nets could be damaged by abrasion for up to 20 min before preservation, the net is towed for 20 min, ascending 15 min, and then the collected sample is washed down into the cod end and preserved (Ahlstrom 1976; Smith and Richardson 1977). Considering these variables, I designed a net treatment to simulate shipboard procedures. For the treatment, seawater was circulated over a single larva in a submerged net container. (Small larvae, 4-7 mm, were treated in groups of 10.) To obtain conservative results, the water temperature was cool, 13° C, and the net-treatment time varied: 5, 10, 15, and 20 min. The net-treatment time included the pipetting and measuring as well as the time in the net. After net treatment, larvae were preserved; I equate these net-treated and preserved larvae with field-collected larvae (Figure 1).

RESULTS

Live Body Parts

Head length, body depth, and eye diameter were examined as functions of standard length for live northern anchovy larvae (Figure 2, Table 1). On a double logarithmic scale (Figure 2) both head length and body depth relationships show curvature, but the eye diameter relation appears to be nearly linear. According to Zweifel,[3] the simple allometric body part relationships used for juvenile and adult fish are not adequate for describing body part relationships of larval fish, except for very limited ranges of size or age. Therefore, I assumed that the larval body proportions (y) change continuously during growth, varying according to a nonlinear allometric growth model,

$$\ln y = a - b(c - \ln x)^d,$$

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Zweiful, J. T. Equations of growth and allometry in larval and adult fish. Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

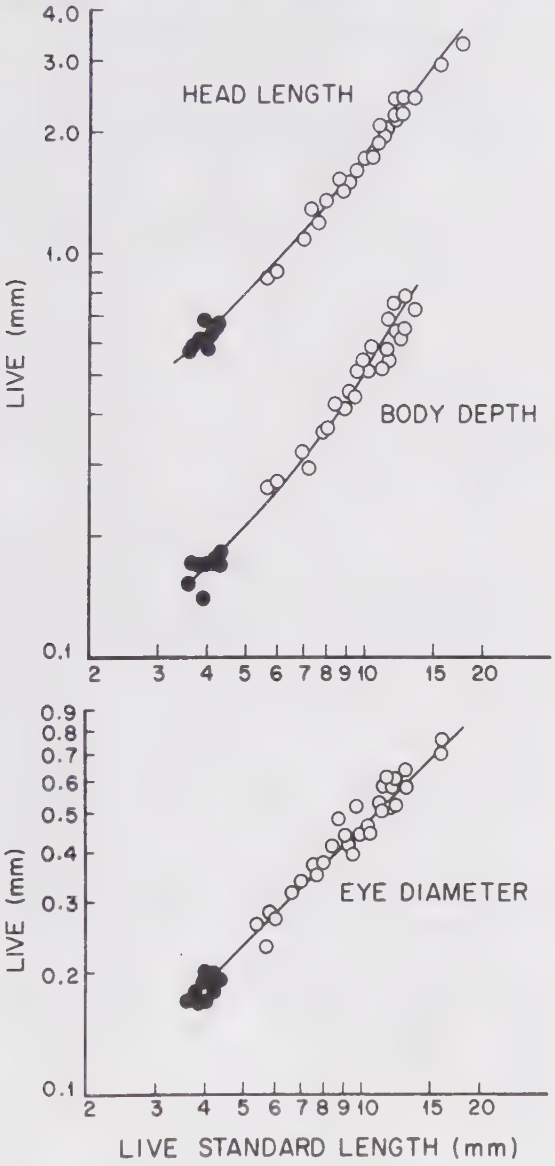

FIGURE 2.—Head length, body depth, and eye diameter as functions of standard length in live northern anchovy larvae. Nonlinear models for live head length and body depth with standard lengths and linear model for eye diameter with standard length are described in the text; estimated parameters are in Table 1. Dots are means of 10 larvae. Circles represent individual fish.

obtained by eliminating time (t) from two Gompertz equations

$$y = y_0 \exp(A_0 [1 - \exp(-\alpha t)] / \alpha) \text{ and}$$
$$x = x_0 \exp(B_0 [1 - \exp(-\beta t)] / \beta)$$

TABLE 1.—Estimated parameters for nonlinear and linear models relating live body part measurements (y) with standard length (x) of northern anchovy larvae.

y	n	a	b	c	d
Head length[1]	86	4.120	2.456	4.189	0.607
Body depth[1]	38	2.922	3.699	3.241	0.389
Eye diameter[2]	44	−3.021	0.976		

[1] $\ln y = a - b\,(c - \ln x)^d$.
[2] $\ln y = a + b \ln x$.

(Zweifel footnote 3). a corresponds to the natural logarithm of the asymptotic size of y; c represents the natural logarithm of the asymptotic size of x (standard length); and d is the ratio of the decay parameters α and β in the individual Gompertz growth curves. The parameter b has no simple biological interpretation except when the decay parameters are equal ($d = 1$); in this case the equation is reduced to a simple allometric growth model. The model was fit to the observed head length and body depth measurements using Marquardt's algorithm for fitting nonlinear models (Conway et al. 1970). The equations (Table 1) gave a good fit to the data (Figure 2). The relation between eye diameter and all treatments is discussed in the section on Eye Diameter.

Laboratory Shrinkage

For northern anchovy larvae preserved in Formalin, the ratio of preserved to preceding live size for standard length (Figure 3), head length, and body depth did not increase with length; i.e., shrinkage did not decrease with age. The ratio averaged 0.92 for standard length after shrinkage in Formalin, and this relation also held for shrinkage in standard length of northern anchovy, jack mackerel, and Pacific barracuda larvae preserved in Bouin's fixative (Table 2). Shrinkage of other body parts differed among species, but the measurements were not made on all three species in

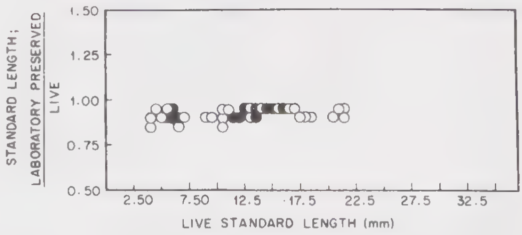

FIGURE 3.—Ratio of subsequent laboratory-preserved standard length to live standard length in northern anchovy preserved in Formalin. Dots are means of two or three larvae. Circles represent individual fish.

TABLE 2.—Shrinkage of laboratory-preserved northern anchovy, jack mackerel, and Pacific barracuda. Ratio is laboratory-preserved size divided by previous live size (1.00 = no shrinkage). Standard length; head length; eye diameter; body depth at the pectoral, BD-1; and body depth at the anus, BD-2. Measurements in millimeters.

		Standard length				Head length				Eye diameter			BD-1			BD-2		
Species	Fixative	No.	Range	Ratio	SD	No.	Range	Ratio	SD	Range	Ratio	SD	Range	Ratio	SD	Range	Ratio	SD
Northern anchovy	Formalin	61	3.9 -21.6	0.92	0.03	23	0.58-2.41	0.91	0.07	0.17-0.61	1.05	0.08	—	—	—	0.14-0.82	0.90	0.10
	Alcohol	26	3.7 -19.0	1.00	.04	—	—	—	—	—	—	—	—	—	—	—	—	—
	Bouins[1]	224	3.8 -15.7	.92	.00	—	—	—	—	—	—	—	—	—	—	—	—	—
Jack mackerel	Bouins	45	3.25-3.90	.92	.03	43	0.74-0.97	.82	.04	0.26-0.33	.90	.06	0.48-0.67	0.75	0.05	0.20-0.26	.75	.05
Pacific barracuda	Bouins	54	3.75-5.23	.92	.02	56	1.00-1.63	.79	.05	0.30-0.48	.82	.04	0.58-0.96	.75	.04	0.24-0.41	.77	.05

[1] P. Paloma, Fishery Biologist, National Marine Fisheries Service, La Jolla, Calif. Unpubl. data.

the same preservative. Jack mackerel and Pacific barracuda, deeper bodied than northern anchovy at the same length, were preserved in Bouin's fixative, and northern anchovy were preserved in Formalin. Head length, eye diameter, and body depth shrank more in jack mackerel and Pacific barracuda larvae than in northern anchovy larvae (Table 2). Eye diameter of northern anchovy increased in size after Formalin preservation; the increase was significant ($P = 0.058$; paired t-test) but small (0.0145±0.0031 mm).

Alcohol preservation did not cause a change in northern anchovy standard length (Figure 4, Table 2); smaller body parts were not measured because alcohol distorted the larvae and they were extremely difficult to remeasure after preservation.

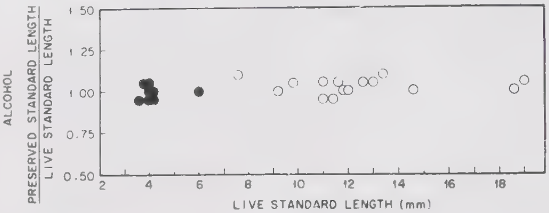

FIGURE 4.—Ratio of subsequent laboratory-preserved standard length to live standard length in northern anchovy preserved in alcohol. Dots are means of 10 larvae. Circles represent individual fish.

Net-Treatment Shrinkage

Shrinkage of net-treated larval northern anchovy varied with handling time and fish size (Ta-

TABLE 3.—Shrinkage in standard length (millimeter) of northern anchovy larvae after net handling for four time intervals (X_2). Ratio (R) = mean net standard length (X_1) divided by mean live standard length (L). Ratio of 1.00 = no shrinkage.

		Mean size		Ratio			Mean size		Ratio	
Live size	n	Live	5 min net	Observed	Estimated[1]	n	Live	10 min net	Observed	Estimated[1]
4.00- 5.99	3	4.27	3.46	0.81	0.84	8	4.40	3.55	0.81	0.81
6.00- 7.99	3	7.57	6.87	0.91	0.90	9	7.17	5.99	0.84	0.85
8.00- 9.99	5	9.02	8.16	0.90	0.92	11	8.87	7.71	0.87	0.87
10.00-11.99	9	10.98	10.21	0.93	0.94	21	11.11	9.85	0.89	0.89
12.00-13.99	6	12.63	12.12	0.96	0.95	29	12.90	11.58	0.90	0.90
14.00-15.99	6	14.60	13.83	0.95	0.96	18	14.85	13.45	0.91	0.92
16.00-17.99	2	16.70	15.80	0.95	0.97	11	16.65	15.22	0.91	0.93
18.00-19.99	4	19.20	18.73	0.98	0.98	11	18.93	17.71	0.94	0.94
20.00-21.99	3	21.10	20.67	0.98	0.99	7	20.80	19.71	0.95	0.95
22.00-23.99	—	—	—	—	—	2	22.75	21.50	0.95	0.96
24.00-25.99	1	24.70	24.50	0.99	0.99	2	24.85	24.10	0.97	0.97
26.00-27.99	1	26.70	26.00	0.97	0.99	1	26.70	25.50	0.96	0.97

		Mean size		Ratio			Mean size		Ratio	
Live size	n	Live	15 min net	Observed	Estimated[1]	n	Live	20 min net	Observed	Estimated[1]
4.00- 5.99	2	4.22	3.41	0.81	0.80	—	—	—	—	—
6.00- 7.99	2	7.35	6.20	0.84	0.83	1	7.50	6.50	0.87	0.82
8.00- 9.99	4	8.96	7.55	0.84	0.84	—	—	—	—	—
10.00-11.99	5	11.44	9.84	0.86	0.86	3	11.73	10.30	0.88	0.85
12.00-13.99	4	12.85	11.29	0.88	0.88	1	13.70	11.50	0.84	0.86
14.00-15.99	7	14.57	12.73	0.87	0.89	6	14.60	12.55	0.86	0.87
16.00-17.99	4	16.57	14.53	0.88	0.90	2	16.70	14.30	0.86	0.88
18.00-19.99	5	19.22	17.72	0.92	0.92	5	19.22	17.22	0.90	0.90
20.00-21.99	3	21.10	19.67	0.93	0.93	3	21.10	19.37	0.92	0.91
22.00-23.99	1	23.50	21.40	0.91	0.94	1	23.50	21.40	0.91	0.92
24.00-25.99	1	24.70	23.40	0.95	0.94	1	25.00	23.80	0.95	0.93
26.00-27.99	1	26.70	24.60	0.92	0.95	—	—	—	—	—

[1] Estimated ratio = $\ln X_1 - \ln L$; Equation (4), see text and Table 4.

ble 3). In larvae 6 mm SL or less, maximum shrinkage (19%) occurred after 5-10 min treatment in the net; larvae were usually dead at the end of the treatment. Older larvae shrank throughout the 20-min period and were often alive at the end. For example, 18-22 mm larvae were 2% smaller after 5 min and 8-10% smaller after 20 min in the net. Further net treatment of larger larvae caused an additional 1-2% shrinkage. Figure 5 shows that measurable shrinkage decreases for older, larger larvae, and that the ratio (R) of the size of net-treated (X_1) to live (L) size larvae rises rapidly from about 0.7-0.8 at 4 mm SL to 0.9 by 11-12 mm SL. Although shrinkage appears nearly constant for larvae from 12 to 22 mm (Figure 5), I measured few older, larger larvae. Conceptually, shrinkage is probably related to the degree of ossification; ossification of northern anchovy vertebrae begins at 14 mm SL and is complete at transformation, about 35 mm (E. H. Ahlstrom[4]). At transformation, shrinkage should be negligible or zero, and the ratio should approach an asymptote of one. To characterize this relationship, I used the equation

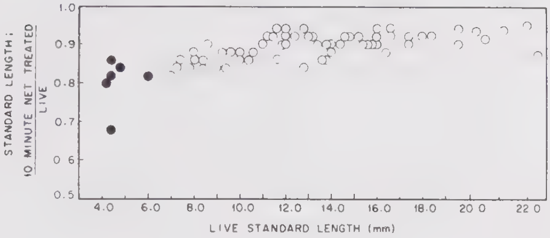

FIGURE 5.—Ten-minute net-treated shrinkage of standard length as a function of size for northern anchovy larvae. Dots are means of 10 larvae. Circles represent individual fish.

$$R = \exp[(-f_1)\exp(-f_2 X_1)]. \tag{1}$$

Equation (1) may be transformed so that the double logarithm of R is a linear function of size, X_1, i.e.

$$\ln[-\ln(R)] = \ln f_1 - f_2 X_1. \tag{2}$$

For standard length measurements, the parameters of Equation (2) were estimated for each of the four net-treatment periods as shown below:

Net-treatment time = t	*ln* f_1	f_2
5	−1.3436	0.1209
10	−1.2708	0.0752
15	−1.2479	0.0509
20	−1.3759	0.0430

The logarithm of f_2 is linear with net-treatment time, i.e.

$$f_2 = g_1 t^{g_2}, \tag{3}$$

while f_1 shows no trend. Combining these two relationships, i.e., R with size (Equation (1)) and f_2 with time (Equation (3)), and inverting the equation to solve for live size in terms of treated larvae, the resultant relationship is

$$\ln L = \ln X_1 + P_1 \exp(-P_2 X_1 X_2^{P_3}) \tag{4}$$

where L is live size, $P_1 = f_1$, $P_2 = f_1 g_1$, $P_3 = g_2$, X_1 is treated size, and X_2 is time (t) in minutes. Equation (4) was then fit directly using a nonlinear fitting procedure (Conway et al. 1970) to obtain the final parameter estimates. The same procedure for estimating parameters and fitting equations was followed for shrinkage of head length and body depth. All equations gave a good fit to the observed data (Figure 6, Table 3); estimates of the parame-

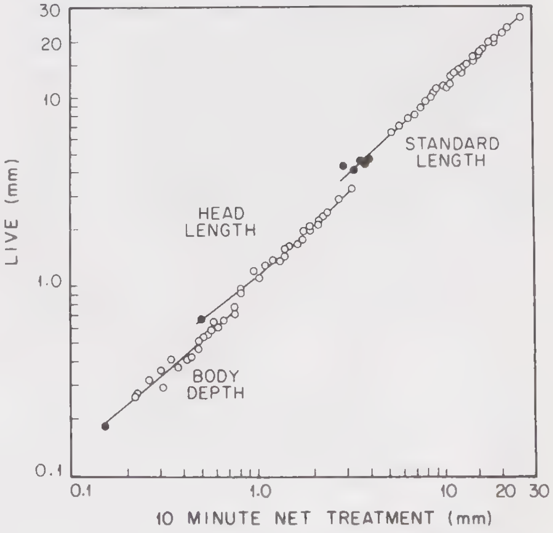

FIGURE 6.—Fit of models (Equation (4)) describing net-treatment shrinkage of larval northern anchovy body parts. Estimates of parameters for models are given in Table 4. Models predict live size from net-treated size.

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[4] E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1978.

TABLE 4.—Estimated parameters for models that predict live northern anchovy body part size (L) from net-treated size (X_1).

Model[1]	P_1	P_2	P_3
Standard length	0.289	0.434	−0.680
Head length	0.177	3.858	−0.605
Body depth	0.413	29.746	−0.620

[1] Equation (4), see text.

ters for the standard length, head length, and body depth models are given in Table 4. These equations can be used to estimate live size of each body part from measurements of northern anchovy larvae after net capture.

Preservation Shrinkage (After Net Treatment)

After larvae shrank during net treatment, additional shrinkage caused by Formalin was nearly a constant proportion of length (Figure 7). The ratio of preserved length to net-treated length (Figure 7) may decrease slightly (i.e., shrinkage may increase) with increasing fish size, but this slight decrease has no practical significance for length calibration of larvae taken in routine plankton samples. Because ossification begins at 14 mm SL, I expect large fish would shrink less, not more, than small fish. The overall mean ratio (preserved size/size after each timed-net treatment) of 104 standard length measurements was 0.9668 ± 0.0020; percent shrinkage of the other body parts was the same as standard length shrinkage. I recommend using 3% shrinkage for all body parts in Formalin after net treatment. Preservation in alcohol after net treatment did not cause further shrinkage (only standard length measured).

To adjust the shrinkage models (Table 4) to predict live size from net-treated and Formalin-preserved size (equivalent to field-collected larvae), the preserved size is multiplied by 1.03. No adjustments are needed for alcohol-preserved samples.

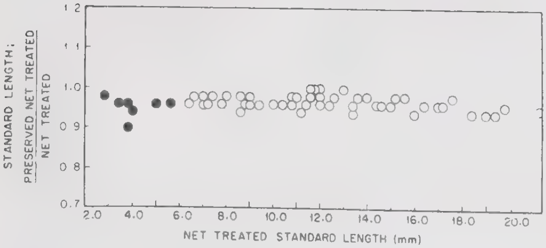

FIGURE 7.—Size specific shrinkage of northern anchovy larvae preserved in Formalin after 10-min net treatment. Dots are means of 10 larvae. Circles represent individual fish.

The difference in shrinkage between laboratory-preserved larvae and net-treated and preserved larvae of the same initial live size decreased with age. For example, 3 mm larvae that were net treated and preserved in Formalin shrank 15% more in standard length than 3 mm larvae that were laboratory preserved in Formalin, but shrinkage of 20 mm larvae was the same for both treatments (Table 5). Shrinkage of laboratory-preserved larvae in Formalin probably decreases to something <8% (Table 5) as the skeleton develops and ossification occurs. Formalin preservation of 90 mm and larger salmon, *Oncorynchus* spp., smolts caused 3-4% shrinkage in length (Parker 1963). Laboratory shrinkage of northern anchovy after transformation may be similar; thus, shrinkage of net-collected and preserved northern anchovy >35 mm (Table 5) should be similar to shrinkage of laboratory-preserved fish >35 mm.

TABLE 5.—Comparison of standard length for live (L), laboratory-preserved and net-treated northern anchovy larvae (X_1). Numbers in parentheses are preserved length divided by live length (ratio of 1.00 = no shrinkage).

Live size (mm)	Estimated preserved size (mm)			
	Laboratory[1]		Net-treated[2]	
	Alcohol	Formalin	Alcohol	Formalin
3	3 (1.00)	2.76 (0.92)	2.38 (0.79)	2.31 (0.77)
5	5 (1.00)	4.59 (0.92)	4.10 (0.82)	3.98 (0.80)
10	10 (1.00)	9.18 (0.92)	8.77 (0.88)	8.51 (0.85)
15	15 (1.00)	13.78 (0.92)	13.81 (0.92)	13.40 (0.89)
20	20 (1.00)	18.37 (0.92)	18.99 (0.95)	18.42 (0.92)
25			24.21 (0.97)	23.48 (0.94)
30			29.40 (0.98)	28.52 (0.95)
35			34.56 (0.99)	33.52 (0.96)
40			39.68 (0.99)	38.49 (0.96)
45			44.77 (0.99)	43.43 (0.97)
50			49.84 (1.00)	48.34 (0.97)

[1] Includes 30 s handling time; no shrinkage in alcohol and 8% shrinkage in Formalin (see text).

[2] Estimated preserved size calculated from Equation (4) for 10 min net treatment; size adjusted for 3% additional shrinkage in Formalin (see text and Table 4).

Eye Diameter

Netting live larvae for 10 min caused the eye diameter to shrink an average of 0.0443 ± 0.0069 mm, and Formalin preservation after net treatment caused an increase in eye diameter that averaged 0.0177 ± 0.0046 mm. The increase in eye diameter after preservation was similar to the increase after preservation noted for eye diameter of laboratory-preserved larvae. The t-tests for paired data ($n = 23$) showed that in all cases the differences between treatments (live, net treated, and preserved) were significant ($P<0.01$). Even though these differences were significant, the small changes in eye diameter size caused by net treating and preserving probably are not important for calibration of size of field-collected larvae. Thus eye diameter should be a useful parameter for estimating average live standard length of field-collected larvae (Table 1).

DISCUSSION AND CONCLUSION

The causes of antemortem shrinkage of fish larvae are not completely understood. Before death, appearance of the body changes from translucent to opaque. This phenomenon is an indicator of ensuing death of larvae in rearing experiments. Autolysis, digestion of tissues by their own enzymes, is occurring during this antemortem period (Theilacker 1978), and the enzymatic action on proteins may cause denaturation, thus the color change and shrinkage. Shrinkage also may be caused by an osmoregulatory problem. An inability to osmoregulate may develop from loss of mucus by abrasion after contact with a surface. The internal osmolar concentration of another clupeoid larva, Pacific sardine, *Sardinops sagax*, is 0.24 M and that of seawater 0.56 M (Lasker and Theilacker 1962). If a larva were unable to osmoregulate, this difference in osmolarity would cause it to lose fluid and shrink.

The amount of shrinkage that occurred before larvae were killed in a preservative was dependent on larval fish size and the extent of "handling" (measuring and netting). The elapsed time of surface contact was the main determinant of final length. This was especially noticeable while measuring small, 3-7 mm larvae. As larvae increased in size and ossification progressed, net-treatment shrinkage decreased.

Preserving larvae after handling caused additional shrinkage that was a constant proportion of size. Laboratory-preserved shrinkage in Formalin included a 30 s handling time; shrinkage in Formalin was constant at 8% and independent of size. Preserving larvae that had been retained in a net caused an additional 3% shrinkage; the additional shrinkage was nearly a constant proportion of size.

Farris' (1963) results on shrinkage of laboratory-preserved, 3-6 mm yolk-sac Pacific sardine larvae agree with my results. He found Formalin shrinkage of standard length ranged between 7 and 11%, similar to the 8% shrinkage for laboratory-preserved northern anchovy in my study. Rosenthal et al. (1978) reported a 16% shrinkage of newly hatched, 2 mm larvae of the sea bream, *Chrysophrys major*. The larvae were anesthesized with MS-222 and measured with a projector prior to preservation in Formalin. It appears that handling of the sea bream was minimal; however, MS-222 has been reported to interfere with osmoregulation (Parker 1963), and an inability to osmoregulate would cause a greater shrinkage. Blaxter (1971) reported on a net-shrinkage experiment that was similar to my study. After his net treatment, mean live size of 22 herring larvae (10.77 mm) decreased by 17%; Formalin fixation caused an additional 3-5% shrinkage for a total of 20-22%. He noted the larvae were dead after netting, but the elapsed time is unknown. In this study, the netted 11 mm northern anchovy were usually dead after 20 min, and the total shrinkage of the 20-min treated 11 mm northern anchovy was about 18%, similar to Blaxter's experiment.

If the larvae to be measured are badly damaged or partially digested, the models generated in this study, which describe live body proportions and shrinkage, could be used to estimate average fish length from size of head or eye. Packard and Wainwright (1974) found that eye diameter of young herring (up to 100 mm) was a useful reference parameter for estimating both size and weight. Because eye diameter of northern anchovy changed little during netting and preservation, eye diameter may be a useful parameter for estimating average live size of field-collected larvae. However, use of eye diameter to estimate live standard length assumes that the relation between eye diameter and standard length is the same for laboratory-reared and field-collected larvae. Balbontin et al. (1973) and Blaxter (1976) have shown that morphological differences exist between reared and wild fish of the same length, thus the assumption, that the body forms of reared and wild northern anchovy larvae are similar, may be invalid. However, as I have shown in this study, the method of handling larvae prior to preservation causes shrinkage differences that could be interpreted as morphological differences.

The most important use of the shrinkage models is to predict live size, and thus age, of sea-collected northern anchovy larvae so that results from laboratory larval fish studies can be related to the sea. Use of the standard length shrinkage model (Table 4) should give the best estimate of live size for field collected larvae. The standard length model can probably be applied to shrinkage of all clupeidlike larvae if the patterns of calcification are similar.

FORTRAN computer programs for the nonlinear models are available at the Southwest Fisheries Center La Jolla Laboratory.

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NOTES

REARING CONTAINER SIZE AFFECTS MORPHOLOGY AND NUTRITIONAL CONDITION OF LARVAL JACK MACKEREL, *TRACHURUS SYMMETRICUS*

Container size may be a critical variable in the rearing of marine fish larvae. Northern anchovy, *Engraulis mordax*, grew faster in 500 l than in 10 l containers (Theilacker and McMaster 1971), and Blaxter (1976) suggested that growth of laboratory-reared fish may depend on space available in tanks as well as food supply and fish density. On intuitive grounds, large containers are preferable for rearing studies but small containers are often used because fewer food organisms are required, treatments can be replicated easily, and daily mortality can be easily monitored. Thus, information is needed on the extent container size affects results of laboratory studies on marine larvae. In this paper, I compare the growth, morphology and nutritional condition of jack mackerel, *Trachurus symmetricus*, larvae reared in 10 l and 100 l containers.

Methods

I collected jack mackerel eggs by towing a 1 m (0.505 mm mesh) plankton net just below the sea surface 61 km off southern California in May 1976. Sea surface temperature was 15.3° C. I sorted and staged normally developing eggs from the plankton and stocked eggs of the same stage at 5/l into 10 l and 100 l black circular rearing containers containing 5 μm filtered seawater at 15.0° C and a light cycle of 12 h light and 12 h dark. I used two treatments for each container size, one fed and the other unfed. Data from the 100 l treatments were reported earlier (Theilacker 1978). Larval diet consisted of a naked dinoflagellate, *Gymnodinium splendens* (50/ml), a rotifer, *Brachionus plicatilis* (30-40/ml), and a copepod, *Tisbe* sp. (1-2/ml). This feeding method has been described previously (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976).

Larvae began to eat 5 d after hatching. I sampled 5-30 larvae daily from fed and starved treatments beginning on day 6 and preserved the larvae in Bouin's solution. Four to five weeks after preservation, I measured standard length (SL, tip of upper jaw to perpendicular at end of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ED), body depth at the pectoral fin (BD-1), and body depth at the anus (BD-2). Shrinkage of jack mackerel body parts in Bouin's solution was as follows: SL, 8%; HL, 18%; ED, 10%; BD-1 and BD-2, 25% (Theilacker 1980). (Data in Table 1 are preserved measurements.) After measurement, I used standard techniques (Theilacker 1978) to prepare larvae for histological examination.

I examined the tissue microstructure of all larvae in fed and starved treatments to determine whether larvae were eating or starving. The onset of starvation in jack mackerel larvae is characterized by a change in the acinar arrangement of pancreatic cells and a sloughing of mucosal cells from the midgut into the lumen (Theilacker 1978). I graded these characteristics of the pancreas and gut and classified individual larval nutritional condition as "healthy," "intermediate," or "starved" (Theilacker 1978). Because histological assessments of larval condition are based on tissue microstructure, these assessments are independent of larval size.

Results

Diameter of jack mackerel eggs collected for this study averaged 1.0 mm. Larvae hatched at 2.45 mm SL (preserved) on day 0 and began to eat at 3.35 mm SL at age 5 d when most yolk was absorbed.

Fed larvae were larger in 100 l than in 10 l containers on each day after the onset of feeding (day 5), but statistically significant differences in size among larvae in the large and small containers did not occur until the larvae had fed for 4 d, age 9 d ($P = 0.002$; Hotelling T^2 multivariate analysis; Table 1).

Among groups receiving no food, larvae in 10 l containers were larger than those starved in 100 l containers at age 8 d, third day of starvation ($P = <0.001$; Hotelling T^2 multivariate analysis; Table 1.) Also, starved larvae in small containers survived 2 d longer than those in large containers, 10 d versus 8 d.

Nutritional condition of fed larvae reared in 10 l and 100 l containers was similar for 5 feeding days,

TABLE 1.—Daily mean body measurements of fed and starved jack mackerel larvae maintained in 10 l and 100 l containers.

Body parts[1]	Day 6				Day 7				Day 8				Day 9				Day 10				Day 11	
	10		100		10		100		10		100		10		100		10		100		10	
	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD
FED																						
Standard length	3.30	0.16	3.35	0.11	3.43	0.05	3.48	0.13	3.38	0.19	3.56	0.13	3.37	0.13	3.83	0.24	3.35	0.21	3.72	0.20	3.35	0.15
Head length	.67	.03	.70	.03	.73	.02	.74	.04	.73	.05	.77	.03	.71	.03	.85	.06	.75	.07	.85	.07	.76	.06
Eye diameter	.23	.02	.25	.02	.26	.01	.26	.01	.26	.02	.29	.02	.25	.02	.32	.02	.27	.02	.31	.03	.25	.01
Body depth-1	.40	.02	.43	.11	.48	.03	.48	.03	.48	.04	.52	.04	.48	.04	.59	.04	.46	.06	.58	.06	.47	.03
Body depth-2	.18	.01	.20	.05	.19	.01	.20	.02	.19	.02	.22	.02	.19	.02	.25	.01	.20	.02	.23	.02	.18	.01
n	4		15		5		15		5		15		5		10		17		15		7	
[2]*P*	0.463				0.523				0.109				0.002				0.001					
STARVED																						
Standard length			3.31	0.11	3.27	0.15	3.35	0.13	3.29	0.12	3.04	0.17	2.99	0.33			3.07	0.21				
Head length			.66	.04	.68	.03	.69	.02	.71	.03	.64	.04	.65	.04			.66	.05				
Eye diameter			.24	.02	.24	.02	.25	.01	.24	.02	.23	.01	.24	.01			.25	.02				
Body depth-1			.41	.03	.40	.03	.42	.02	.38	.02	.42	.03	.36	.02			.35	.02				
Body depth-2			.18	.02	.18	.01	.18	.01	.17	.01	.17	.01	.17	.01			.17	.01				
n			14		28		15		15		19		16				26					
[2]*P*					0.351				<0.001													

[1]Preserved measurements.
[2]Probabilities for equal body measurements between container sizes (multivariate analysis; Hotelling T^2).

TABLE 2.—Daily histological condition of fed and starved jack mackerel larvae maintained in 10 l and 100 l containers.

Histological grade[1]	FED											STARVED						
	Day 6		Day 7		Day 8		Day 9		Day 10		Day 11	Day 6	Day 7		Day 8		Day 9	Day 10
	10	100	10	100	10	100	10	100	10	100	10	100	10	100	10	100	10	10
Starved (1.00-1.66)	0	1	0	0	1	1	1	1	8	1	3	7	20	6	12	15	8	22
Intermediate (1.67-2.33)	3	1	0	2	0	3	0	0	4	2	0	3	3	6	0	1	1	2
Healthy (2.34-3.00)	1	12	5	13	3	11	4	9	4	12	3	3	1	2	0	2	0	0
Average grade	2.25	2.77	2.90	2.80	2.50	2.62	2.60	2.80	1.80	2.65	2.08	1.88	1.32	1.71	1.00	1.25	1.11	1.08
[2]*n*	4	14	5	15	4	15	5	10	16	15	6	13	24	14	12	18	9	24
[3]*P*	>0.10		>0.10		>0.10		>0.10		>0.05				>0.10		>0.10			

[1]Theilacker (1978).
[2]Total number of larvae within each treatment does not agree with Table 1, as several larvae were lost during the microtechnique procedure.
[3]Probabilities for equal histological grades between container sizes (two-sample nonparametric Kolmogorov-Smirnov Test).

until age 10 d when it was significantly better in the large containers ($P = <0.05$; Kolmogorov-Smirnov Test; Table 2); fewer larvae were classed as "starved" in the larger containers. For larvae given no food, no difference existed in condition of larvae between large and small containers.

Fed larvae died at ages 12-13 d in the small containers. On day 13 there was also a major mortality in the large containers, but a few larvae survived through the juvenile stage, and one fish lived for 49 d, 31 mm SL. I did not sample these survivors unless they appeared to be dying. For jack mackerel there is no well-defined metamorphosis; the juvenile stage begins at the completion of fin formation, 12-16 mm (Ahlstrom and Ball 1954). In the large container, fin formation was complete at 14 mm, 39 d of age ($n = 1$); size at age for this laboratory-reared fish was similar to field-collected fish (age of wild fish is being determined by reading daily growth increments in otoliths (Methot[1])).

Conclusions

Relating experimental results from laboratory to field conditions must be done with caution. Blaxter (1975) compared morphology, chemistry, and physiology between reared and wild larvae and concluded that results on growth, nutrition, and mortality of laboratory-reared larvae should not be related to the field. My study shows that jack mackerel larvae reared with food in 10 l containers were smaller and in poorer nutritional condition than larvae reared in 100 l containers. These container-effects occurred at an early age, i.e., morphological differences were evident 9 d after hatching and histological differences 10 d after hatching. Larvae may grow faster and show fewer signs of starvation in large containers because: 1) there is a lower probability of damage from contact with the walls; and/or 2) the same prey density in a larger container may permit the formation of larger food patches and thereby elevate the actual density of food encountered by the larvae; and/or 3) water chemistry in larger containers may be more favorable.

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[1]R. Methot, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. January 1980.

In contrast to results of the feeding experiments, larvae starved in 10 l containers survived 2 d longer and were larger at age 8 d than those in 100 l containers. This indicates that activity may be affected by container size. Larvae in small containers may be less active, consume energy reserves less rapidly, and therefore live longer without food.

The effect of container size on growth, nutritive condition, and possibly activity in jack mackerel larvae, emphasizes the caution that must be exercised when relating results from laboratory to field conditions. The large container may have had no effect on growth and development of jack mackerel, but survival was poor. Further studies are needed to determine the minimum container size required to simulate natural conditions in the laboratory. Because spatial requirements of larval fish depend on locomotory patterns as well as on genetic adaptations to life near solid surfaces (Kinne 1977), optimum container size will probably vary with fish species. In larval fish experiments, container size is a variable that must be considered with temperature, light, food type and availability, and stocking density.

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INTRODUCTION

Good and poor year classes of fish may be determined during the larval stage by physical events that act upon larvae directly or indirectly by controlling their food supply (Hjort, 1914; 1926). The goal of this workshop is to evaluate our ability to identify and monitor these physical events, at appropriate scales, which might facilitate forecasting larval fish survival. Larval survival depends not only on environmental variables and prey availability at first feeding but also on a suite of species specific behavioural and physiological characteristics. Thus, minimum food concentrations needed to initiate feeding and promote larval fish survival will vary among species due to interspecific differences in egg size (hence development at hatching), resistance to starvation, feeding strategies, growth rates, growth efficiencies, and metabolic demands. Therefore, these food concentrations and other input parameters in models designed to predict survival and recruitment must incorporate species-specific functions. Presented here are pertinent life history, behavioural and physiological parameters of four important pelagic representatives of related species of the California and Peru Currents, as well as twelve predominantly demersal species of the north Atlantic Ocean (Table 1).

Table 1

EARLY LIFE HISTORY

Species	Range	Spawning season (peak)	Type	Egg diameter (mm) Range	Incubation Days	Incubation °C	Hatching Size mm	Hatching dry wt µg	Yolk absorption Days from hatching	Yolk absorption °C	Onset of feeding Days from hatching	Onset of feeding °C	Irreversible starvation (a) Days from hatching (b) Days from Yolk Abs.	Irreversible starvation °C	Metamorphosis Days from hatching	Metamorphosis °C	Metamorphosis Length (mmSL)
Limanda ferruginea (Yellowtail flounder) 1.	Gulf of St. Lawrence to Virginia	March-Aug.	Pelagic	0.88 0.79-1.01	5-7	10	2.0-3.5	16	4-5	10	4-5	10					14
Limanda limanda (Dab) 2.	North Sea English Channel	March-June (Feb.-April)	Pelagic	0.65-0.95			2.6				Yolk absorption						
Pleuronectes platessa (Plaice) 3.	North Sea English Channel to Norwegian Rinne Skagerrate	Dec.-April	Pelagic	2.0 1.7 - 2.2	18	7-11	5.0-6.7	151	6-10	7-11	4-6	7-10	6-8$^{(b)}$	8-11	40-75	7-11	9-13
Pseudopleuronectes americanus (Winter flounder) 4.	Northern Labrador to Georgia	Dec.-May	Demersal	0.80 0.71-0.96	17-25	3	2.3-3.5	10-30	9	8	5	8	5-7$^{(b)}$	8	58	8	6.5-9
Paralichthys dentatus (Summer flounder) 5.	Maine to Florida	Oct.-April	Pelagic	1.04 0.90-1.13	[illegible]	17	[illegible]		3-4	16	4	16	6-7	16	47-56	16	[illegible]
Solea solea (Sole) 6.	North Sea English Channel	April-June	Pelagic	1.0 - 1.5	8	10-12	3.2-3.7		7						42-56	10-12	9-10
Achirus lineatus (Lined sole) 7.	Florida and Gulf of Mexico to Uruguay		Pelagic		1	28		21.8	3	28	2	28	3-3.5	28	16	28	4-5
Stenotomus chrysops (Scup) 8.	Nova Scotia to Eastern Florida	May-July	Pelagic	0.94 0.85-1.15	1.5	22	2.0		3	22	3						10
Archosargus rhomboidalis (Seabream) 9.	New Jersey to Rio de Janeiro	Sept.-May	Pelagic		1	26	1.8-[illegible]	27.0	2	26	1.5	28	2.5	28	9-11	23-24	7-9
Gadus morhua (Cod) 10.	North Atlantic Coastal Waters	Dec.-April	Pelagic	1.52 1.10-1.72	12	5.5	3.3-5.7		6	7.2	~5	7	5$^{(b)}$	7	52	7	10
Melanogrammus aeglefinus (Haddock) 11.	North Atlantic Biscay to Barents Sea Newfoundland to Cape Cod	Feb.-June	Pelagic	1.46 1.10-1.67	17	5.5	2.0-4.1		7	7	~5	7	5$^{(b)}$	7	42-49	7	10
Clupea harengus (Atlantic herring) 12.	Greenland-Cape Hatteras Iceland-Gibraltar	July-Nov.; May (Sept. & May)	Demersal	1.0 - 1.4 0.36-3.0	15 (Maine, Downs)	8	4.0-10.0	90 (50-220)	6 (Firth of Clyde) 15-20(W.Baltic)	8	2-6 (Firth of Clyde) 15-20 (Baltic)	8	6$^{(b)}$(Firth of Clyde) 12-22$^{(a)}$	8-12 8	112-168	8-12	30-40
Sardinops sagax (Pacific sardine) 13.	Southern Alaska to Gulf of California	Feb.-July (May-June)	Pelagic	1.7	2.8	15	3.75	36			4-5	16			45-50		31-35

Table 1 - Cont'd.

Species	Range	Spawning season (peak)	Egg Type	Egg Diameter (mm) Range	Incubation Days	Incubation °C	Hatching Size mm	Hatching Dry wt µg	Yolk absorption Days from hatch	Yolk absorption °C	Onset of feeding Days from hatch	Onset of feeding °C	Irreversible starvation (a) Days from hatch (b) Days from Yolk Abs.	Irreversible starvation °C	Metamorphosis Days from hatch	Metamorphosis °C	Length (mmSL)
Engraulis mordax (Northern anchovy) 14.	Northern Baja California to Arctic Alaska and Japan	Jan.–July (March–May)	Pelagic	0.66(X)1.35	2–3	16	2.9–3.2	21	4	16	4	15–16	2.5(a) 4.5(b)	16.5 15	50–60		30–40
Engraulis ringens (Anchoveta) 15.	Coasts of Peru and Chile	July–March (Sept. & Feb.)	Pelagic	0.71(X)1.42	0–2.25	14–16	2.19–2.72		3	18	4.5 (3.5–6.0)	18	4.5	18			32
Scomber japonicus (Pacific mackerel) 16.	West coast Alaska to Banderas Bay, Mexico	April–August (May–July)	Pelagic	1.06–1.14	3.6	16	3.1	40	3	19	2–2.5 4	19 16	2(b) 3.5(b)	19 16	25		15
Trachurus symmetricus (Jack mackerel) 17.	Magdalena Bay, Baja California to Southeast Alaska	Feb.–August (May–June)	Pelagic	1.0 0.90–1.02	2–3	15	2.1a/ 2.8b/	34c/			5	15	2.5(b)	15	40		11–16

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5. Martin and Drewry, 1978
6. Blaxter and Staines, 1971; Riley, 1974
7. Houde, 1974, 1977, 1978
8. Johnson, 1978; Colton and Marak, 1969
9. Stepien, 1976; Houde, 1974
10. Hardy, 1978; Laurence, 1978
11. Hardy, 1978; Laurence, 1978
12. Jones et al., 1978; Rosenthal and Hempel, 1969; Bayer and Laurence, 1980; Blaxter and Staines, 1971; Hempel and Blaxter, 1963 (Note: Values vary widely between individual stocks of Atlantic herring; stocks named where known)
13. Lasker, 1962; Lasker, 1964; Ahlstrom, 1943; Ahlstrom, 1966
14. Lasker, 1964; Lasker et al., 1970; Kramer and Zweifel, 1970; Hunter, 1976; Theilacker, unpubl.; Ahlstrom, unpubl.
15. Rojas de Mendiola (this volume)
16. Kramer, 1960; Hunter and Kimbrell, 1980
17. Kramer, 1960; Ahlstrom and Ball, 1954; Theilacker, 1980

a/ 0.90 mm egg

b/ 1.0 mm egg

c/ wt at yolk absorption, day 5

SPAWNING

With the exception of the cod, *Gadus morhua*, the Atlantic species discussed here form localized coastal populations and do not undertake extensive migrations. The stocks of these species are considered to be relatively distinct in their various localities for that reason. Each species has its own preference for bottom terrain, depth and temperature. All undertake at least a short migration before or during their spawning period, most of them toward shallower, inshore waters.

Peak spawning times vary with each species in each locality. Generally, in the northern hemisphere spawning begins in the southern part of the species' range and moves northward as the season advances following the advance of primary production cycles. This is reversed in the southern hemisphere. Spawning times of the four California Current species overlap. Northern anchovy, *Engraulis mordax*, and northeastern Pacific sardine, *Sardinops sagax*, spawn in early spring, and Pacific mackerel, *Scomber japonicus* and jack mackerel, *Trachurus symmetricus*, spawn later. Kramer and Smith (1970) summarized spawning from 1951-1960 in the California Current, 20-300 miles off the coast as follows: Pacific sardine spawning begins in small areas in January off both southern California and Baja California, the centers of the northern and southern subpopulations. Spawning areas continue to expand to the north and south and by May-June spawning is maximum, appearing as one area extending from Point Conception, California to mid-Baja California. Spawning of northern anchovy extends from Point Conception to southern Baja California from January to May; the spawning area decreases somewhat in June and July. Lasker and Smith (1977) could find no relation between amount or location of northern anchovy spawning and changes in temperature or zooplankton production over the spawning area between 1953 and 1960. Pacific mackerel spawning begins in the Spring off southern Baja California, moves north with warming water to southern California in May, June and July. Major spawning of jack mackerel first occurs in March off northern Baja California, and spawning gradually spreads northward off southern California in April and peaks in May and June as the water warms. Thus, between April and July, spawning of the four California Current species overlaps both temporally and spatially.

Frequency

Although little information is available on spawning frequency, some species are known to spawn at intervals during the spawning season. In cod and haddock, *Melanogrammus aeglefinus*, not all of the eggs within the ovary ripen at once; for cod there are at least three and possibly up to eight batches of eggs in a season (Hardy, 1978). Yellowtail flounder, *Limanda ferruginea*, also spawn more than once throughout a prolonged spawning season (Martin and Drewry, 1978). Hunter and Goldberg (1980) give evidence of batch spawning in the northern anchovy with a periodicity of about seven days and perhaps as many as 20 spawnings over the season. Thus, relationships between adult biomass and apparent egg abundance are complex.

EGGS

The eggs of the subject species range in size from 0.65 to 2.2 mm in diameter (Table 1) and, with the exception of anchovy, eggs are spherical. Egg buoyancy varies; most eggs are pelagic except for those of winter flounder, *Pseudopleuronectes americanus*, and herring, *Clupea harengus*. Early-stage pelagic eggs are found in the surface waters but they may descend to mid or bottom depths as development proceeds. Cod eggs are an example of this latter process (Hardy, 1978). Variations in density within the water column may "trap" eggs in their iso-density surfaces or vertical mixing may distribute them throughout the mixed water layer, but most pelagic eggs are found at or near the surface.

Size

Within species, egg size has been shown to decline from spring to summer and vary inverseley with temperature (Ware, 1975). Decreasing egg size with season may be due to a shift in spawning from older to younger females (Ahlstrom, pers. comm.). Within species larger eggs are hypothesized to improve survival by producing larger larvae that are able to swim faster and search a greater volume of water for food (Hunter, in press). However, Hempel and Blaxter (1963) found that within a race of herring, the larvae hatching from large eggs did not survive longer than those from smaller eggs (no food was added), presumably because larger larvae have proportionately higher metabolic demands. But it has been shown that jack mackerel hatched from large eggs can grow twice as fast with the same feeding treatment as those hatched from small eggs (.09-.15 mm/day versus .05 mm/day; Theilacker, 1980a).

Incubation time is a function of egg size and temperature; larger eggs take more time to hatch at similar temperatures (Table 1). Egg size also affects duration of yolk-sac stage (Ware *et al.*, 1980), time to irreversible starvation (Blaxter and Hempel, 1963), and hatching size (Blaxter and Hempel, 1963; Theilacker, 1980a; Eldridge, pers. comm.). Temperature has a significant and reproducible effect on each of these parameters. However, at constant temperature, the influence of differing egg sizes on these parameters may vary; in particular, jack mackerel incubation time, yolk-sac stage, and time to irreversible starvation did not differ between egg sizes (0.9 versus 1.0 mm), yet size at hatching and growth rates did differ (Theilacker 1980a).

LARVAE

At hatching larvae range from 1.89 mm for lined sole, *Achirus lineatus*, to over 6.0 mm for the plaice, *Pleuronectes platessa*, and herring (Table 1). Larvae show varying degrees of development at hatching, but at yolk absorption, the described larvae have pigmented eyes, open guts, and functional mouths if development occurred within the species' optimal temperature range. Most larvae, with the exception of anchovy and sardine, are capable of feeding before their yolk is completely absorbed. There is evidence that when food is present the yolk is absorbed at a constant rate, but if food is not present the rate of utilization begins to decline (Ryland and Nichols, 1975).

At the time of complete utilization of the yolk reserves, larval survival is dependent upon the larva's ability to find and capture sufficient prey. The amount of time a larva can survive without food, before it is too weak to feed and death is inevitable, has been termed the time to "point of no return" (Blaxter and Hempel, 1963). Days to point of no return (irreversible starvation) are quite similar among described Atlantic species and among described California Current species (Table 1). In general, the Atlantic species have one week to capture a critical number of prey organisms for survival and subsequent development. The California Current and tropical Atlantic species have only 2-5 days until irreversible starvation, but they are generally exposed to higher temperatures than the subject Atlantic species. The time to irreversible starvation has been shown to decrease with increasing temperature (Lasker *et al.*, 1970; Hunter and Kimbrell, 1980).

Survival vs starvation

After the yolk has been absorbed, larvae must eat. The locomotory and perceptual capabilities of the larvae, the density of suitable prey and the behavioural patterns of larvae and prey are the important factors that influence feeding, and thus survival and growth. Delaying larval feeding for one or more days after yolk absoption decreases survival and growth rate. For example, starving northern anchovy for three days after they were capable of feeding decreased survival to age 13 days from 70% (for fed larvae) to 20% (for delayed-fed larvae) and decreased size from 7.1 mm standard length (SL) to 4.6 mm SL respectively. Four days of starvation decreased survival at age 13 days to 6% and size to 3.6 mm SL (Theilacker, unpubl.).

Starved northern anchovy larvae were active during the first day without food but activity decreased thereafter; larvae began to sink, head down, but they exhibited avoidance behaviour throughout the four-day starvation period. As anchovy larvae sink, reduction of activity may reduce risk of predation (Hunter, in press). The larvae may also enter an area of higher food concentration or enter cooler water, thus increasing available calories and/or decreasing metabolic demands, thereby increasing probability of survival for a longer time. At the time of irreversible starvation, Pacific mackerel, unlike anchovy and jack mackerel, continue to swim and eat but they cannot eat enough to survive (Hunter and Kimbrell, 1980).

The onset of starvation in anchovy and mackerel larvae is characterized by changes in the histological characteristics of the pancreas, liver and gut (O'Connell, 1976; Theilacker, 1978). The mackerels require two days of eating to repair tissue damaged by one day of starvation, and they do not grow during this period. The gut is the first tissue degenerated by starvation and apparently the last tissue to be repaired (Theilacker, 1980a).

The number of days to irreversible starvation increases with age. For northern anchovy, time to irreversible starvation from the onset of feeding (when the larvae had no body reserves) was 3-4 days (Table 1); at metamorphosis (when the fat level was 30%, dry weight) it was 15 days. Fat levels declined to about 12% in the 15-day starved metamorphosed fish and recovered to the original levels after 5-8 days of feeding (Hunter, 19760. Results were similar for herring larvae; time to irreversible starvation increased from six days at yolk absorption (6 days of age) to 15 days at 88 days of age (Blaxter and Erhlich, 1974).

Swimming modes

The food-searching ability of larvae is a function of their swimming capabilities, activity levels, perceptive distances and their ability to successfully complete the attack sequence on a prey organism.

The dominant swimming mode of larval anchovy is a beat and glide, or intermittant swimming (Hunter, 1972). In contrast, Pacific mackerel (Hunter and Kimbrell, 1980) and jack mackerel beat continuously (Theilacker, unpubl.). Vlymen (1974) has calculated that slow, intermittent swimming is efficient for larval anchovy while Weihs (1974) shows that intermittent swimming is less efficient for mackerels of all sizes. Larval Pacific mackerel swim at more than twice the speed of northern anchovy (.46 versus .2 cm/s; Table 2), owing in part to their differences in swimming mode. Swimming speeds for 6 mm jack mackerel are intermediate between Pacific mackerel and northern anchovy of the same size (Table 2). O'Connell (in press) suggests that the differences in swimming modes between northern anchovy and Pacific mackerel may be due to anatomical differences. The short post-anal tail (thus short flexure) of anchovy is due to their long digestive tract, and the long post-anal tail (thus long flexure) in mackerel is due to their short, compact digestive tract.

Swimming speed

Voluntary swimming (cruising) speeds for young larvae (Table 2) range between 0.1-0.5 cm/s; sardine, anchovy, sole and plaice are at the low end of the range with mackerel and herring at the high end. Variation in experimental methods has produced widely differing results. For example, in forced swimming experiments (Ryland, 1963) plaice swam about 2 to 7 times faster than during voluntary swimming experiments (Blaxter and Staines, 1971; Table 2). Swimming speeds of young larvae in experimental tanks may be comparable to, or typical of, speeds achieved in the field; but container size probably affects activity of older larvae. In particular, Hunter (pers.comm.) has seen 10 mm northern anchovies swim apprxomately 1 m in about two seconds (about 50 cm/s) in a large, deep tank (5 m x 10 m). This is much faster than burst speeds over short distances measured in smaller experimental tanks for northern anchovy (e.g., 15 cm/s; Hunter, 1972).

Although voluntary and sustained swimming speeds are needed to determine routine energy expenditures of larval fish, estimates of burst swimming speeds are essential to determine energy required to capture prey and avoid predators. Both burst speeds for northern anchovy larvae and distance travelled per burst (endurance) increased linearly with length (Webb and Carolla, MS; Table 2); for herring larvae the duration of single bursts decreased with length while the number of bursts per minute increased (von Westernhagen and Rosenthal, 1980). Jack mackerel burst speed and endurance is about twice that of anchovy at the same age (Table 2).

Swimming speeds appear to be inversely correlated with prey density. For example, plaice (Wyatt, 1972) and cod (Ellertsen *et al.*, 1980) increased their swimming activity in the absence of food, and northern anchovy, 4-8 days of age, swam at 0.5 cm/s outside a food patch and at 0,3 cm/s inside a patch (Hunter and Thomas, 1974). Thus, swimming speeds are apparently reduced when food organisms are encountered, and the commensurate expenditure of energy due to swimming activity could conceivably be less in high food concentrations. But it may be that within a food patch the combined energy expended in slow swimming plus attacking prey is greater than energy used outside a food patch for faster swimming (see section on Attack modes). Owing to these observed decreases in swimming speed with increasing prey density, extrapolations to calculate volume of water searched and hence prey density requirements from swimming speeds should be made with caution.

Table 2. Activity -- swimming speeds.

Species	°C	Age	Cruising[1]		Burst		Duration of burst or distance traveled per burst	Reference
		(d; mm; µg)	cm/s	BL/s	cm/s	BL/s		
Sardine	15-18	yolk; 3-5 mm	0.2					Blaxter & Staines
Sardina pilchardus	"	3 wks.	0.3					1971
Herring	8-12	yolk; 6-11 mm	0.4					Blaxter & Staines
Clupea harengus	"	8 wks.	1.4					1971
				2.3		8-10		Blaxter 1969
Northern anchovy	13	3 mm	0.1	.2				Hunter 1972
Engraulis mordax	19	3 mm	0.2	.6				Hunter (in press)
	13	5 mm	0.3	.5				
	19	5 mm	0.5	.9				
	17	15 mm	1.5	1.0				
" "	17	35 mm[2]	3.5	1.0				
	17	80 mm	12.0	1.5				Theilacker (unpubl.)
	17	150 mm	50.0	3.3				
	17	8 mm[3]			3		8-16 ms	Hunter 1972
	17	13 mm[3]			8		8-16 ms	
" "	17	3 mm			7.3[4]	24	1.3 cm/176 ms	Webb & Carolla (MS)
	17	8 mm			11.4[4]	14	3.1 cm/272 ms	
	17	13 mm			15.5[4]	12	5.0 cm/323 ms	
Whitefish[5]	7-15	15 mm	1.5	1.0				Hoagman 1974
Coregonus clupeaformis								
Jack mackerel	16	6.0-6.5 mm	.36 -	0.8		4-6	2-8 cm; 2 s	Devonald (pers.comm.)
Trachurus symmetricus			.72	(0.6-1.2)				
Pacific mackerel	19	3.6 mm	0.46	1.3				Hunter & Kimbrell
Scomber japonicus	"	15.0 mm[2]	5.6	3.8				1980
Large mouth bass	19	2-7 d; 6-7 mm	3-4[6]	4-5				Laurence 1971
Micropterus salmoides								
Plaice[7]	10-12	yolk; 5-7 mm	0.2					Blaxter & Staines
Pleuronectes platessa	"	9-10 mm	1.0					1971
	"	5-7 mm	1.5[8]		4-9[1]	-10	9-15 cm	Ryland 1963
	"	9-10 mm	2.2[8]		9-15[1]	-13	12-36 cm	
	"	25 mm	6.5[8]					
Sole[7]	10-12	yolk; 3-5 mm	0.1					Blaxter & Staines
Solea solea		9-10 mm	0.7					1971
Walleye perch[9]	13	7.5 mm	0.5	0.6				Houde 1969
Stizostedion vitreum vitreum	"	11.0 mm	3.5	3.0				
Yellow perch[9]	13	7.5 mm	1.5	1.8				Houde 1969
Perca flavescens	"	11.0 mm	3.5	3.0				

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[1] voluntary swimming
[2] metamorphosis
[3] attacking prey
[4] mean burst speed = 8.18 L + 4.89; maximum distance traveled = 3.79 + 0.08
[5] no effect of temp. or age
[6] forced swimming; speed sustained for 30 m
[7] 90% decrease in activity at metamorphosis
[8] forced swimming; speed sustained 4-20 s
[9] forced swimming; speed sustained for 1 h

Attack modes

At the onset of feeding there are two basically different larval feeding behaviours, "S" and "C" postures. To illustrate, as northern anchovy sight prey their sinuous body moves into an "S" posture. Then, using their pectorals to move toward the prey, they straighten their body, driving it forward to capture the prey (Hunter, 1972). "S" posture feeding behaviour is also typical for young larvae of engraulids (bay anchovy, *Anchoa mitchelli*; Houde, 1973); clupeoids (Pacific sardine; Schumann, 1965); herring (Rosenthal and Hempel, 1970); and flatfishes (Jones, 1972). In contrast to the "S" posture behaviour, larvae of Pacific mackerel stop swimming and assume a "C" posture when sighting prey, then they open their mouths and lunge toward prey by driving the tail posteriorly (Hunter and Kimbrell, 1980). This "biting-lunge" technique is also typical for larvae of jack mackerel (Theilacker, unpubl.) and cod (Ellertsen *et al.*, 1980), but cod also appear to expand their oral cavity and suck in prey. Some fishes are more energy-efficient and opportunistic. For example, *Sebastes*, the rockfishes, use the "biting-lunge" technique but are less active and wait for prey to swim nearby (Butler, pers. comm.).

Hunter (in press) stresses two other important differences in feeding between northern anchovy and Pacific mackerel: the first, anchovy strike only once at a food particle and mackerel will move backward and persist in striking until successful. The mackerel's persistent feeding strategy is advantageous because the large prey they prefer to eat are harder to capture and less abundant than the smaller prey eaten by anchovy (Hunter, in press). Larval plaice (Blaxter and Staines, 1971), cod (Ellertsen *et al.*, 1980) and jack mackerel (Devonald, pers. comm.) also have been observed moving backward and repeatedly striking at the same particle.

The second important difference in feeding between northern anchovy and Pacific mackerel is that mackerel are cannibalistic at 10 mm (20 days) and larval anchovy are never piscivorous (Hunter, in press). Sibling cannibalism is considered to be a density-dependent disadvantage of patchy spawning (Hunter, in press; Hewitt, 1980). Neither jack mackerel nor Pacific sardine are cannibalistic in the laboratory; whether this is due to behavioural differences or an inability to physically manoeuvre this sort of prey is unknown.

The difference in manoeuvrability between species probably accounts for differences in their feeding success and habits. Initial feeding success is low for herring, 2-6% (Blaxter and Staines, 1971) and northern anchovy, 10% (Hunter, 1972). Winter flounder (Laurence, 1977), bay anchovy, *Anchoa mitchelli*, lined sole (Houde and Schekter, 1980), and big-eye anchovy, *Anchoa lamprotanea*, (Chitty, 1980) also require several days of feeding to establish and improve feeding success. On the other hand, larvae with greater manoeuvrability have relatively high initial feeding success; sea bream *Archosargus rhomboidalis*, (Houde and Schekter, 1980), plaice (Blaxter and Staines, 1971), cod (Ellertsen *et al.*, 1980), Pacific mackerel (Hunter and Kimbrell, 1980), and jack mackerel (Theilacker, 1978) are efficient feeders at the onset of feeding.

For larvae that are ineffective feeders on the first day of feeding, the energy cost of attacking prey must be relatively great. For example, the nutritional condition of first-feeding northern anchovy (determined by histological techniques) was poorer in larvae that had been feeding for one day than in larvae which were starved. Most first feeding northern anchovy larvae were not in a healthy, robust condition until they increased their capture efficiency, usually on the third day of feeding (O'Connell, 1976). On the other hand, the same experimental situation with jack mackerel larvae had opposite results (Theilacker, 1978); fed larvae were always in better histological condition than starved larvae. Thus, jack mackerel are probably more efficient than anchovy at capturing prey on the first and second day of feeding. In addition, yolk reserves in unfed jack mackerel were greater than in fed larvae, again indicating that energy expenditure for non-feeding larvae was larvae was less than for feeding larvae (Theilacker, 1978).

Visual Perception

Most larvae are believed to be purely visual feeders. Perceptive distances may depend on prey movement, orientation in relation to the eye, contrast to the background and illumination. Perceptive ranges for herring even depended on their swimming speed; ranges were greater during slow swimming than fast swimming (Rosenthal and Hempel, 1970). At first feeding, movement of prey does not appear to be a criterion for acceptance, as larvae often eat non-motile foods such as copepod eggs. Distance to the prey and prey size probably are the important factors in prey detection. In all larval fish studies, perceptive distance, usually expressed as a function of body length (BL), has been shown to increase with age/size (Hunter, in press). For example, over an eight-week period, the perceptive distance of plaice increased from 3.5 to 5.5 mm, that of pilchard, *Sardina pilchardus*, increased from 1.0 to 2.5 mm, and of herring from 3.5 to 5.0 mm (Blaxter and Staines, 1971). Average perceptive distances summarized by Hunter (in press) are:

	BL	
herring	0.7-1.0	Rosenthal and Hempel 1970
herring	0.4	Blaxter and Staines 1971
plaice	0.5	Blaxter and Staines 1971
pilchard	0.2	Blaxter and Staines 1971
anchovy	0.4	Hunter 1972
whitefish	0.4-0.7	Hoagman 1974

Most fish larvae feed only during the day, but some larvae feed in dim light, and some may feed at night. Houde and Schekter (1980) noted limited feeding of young bay anchovy, lined sole, and sea bream, at 50 mc. Freshwater larval whitefish, *Coregonus clupeaformis*, feed at one mc (Hoagman, 1974), and Smith *et al.* (1978) mentioned four species that feed at night; rockfish, *Sebastes marinus* (Marak, 1974), sole, *Solea solea* (Blaxter, 1969), plaice (Shelbourne, 1953) and yellowtail flounder. Blaxter (1969) found that feeding became reduced in herring at a light intensity range of 10^{2}-10^{-1} mc and in plaice at 10^{2}-10^{-2} mc.

Increased visual sensitivity probably occurs in northern anchovy when rod recruitment begins begins at about 10-11 mm SL or 20 days of age (O'Connell, in press). Appearance of rods occurs at about the same size in Pacific hake, *Merluccius productus*, (O'Connell, pers. comm.). Thus, older fish may feed at night or in dim light. Indeed, older larvae of plaice were capable of feeding in the dark (Blaxter, 1969). Yet, young Pacific hake (before rod recruitment) and young cod (of unknown rod appearance) feed intensively after sunset (Sumida and Moser, 1980; Ellertsen *et al.*, 1980). The role of bioluminescence should be considered.

Chemical stimuli may be a factor for location of prey by larval fish. For example, herring larvae show increased activity when extracts of *Balanus*, *Artemia* or herring are added to their tank (Dempsey, 1978) and northern anchovy appear to locate dense patches of *Gymnodinium* prior to eye pigmentation (Hunter and Thomas, 1974).

Distribution

Our knowledge of larval distribution in time and space is extremely limited. Diurnal variations in larval distribution are attributed to activity, phototaxis, temperature preference, prey distribution, and current movements. Vertical distribution studies, like most field studies, suffer from the difficulty in determining the importance of net avoidance in sampling. Net avoidance results in fewer larvae collected by day, especially larger larvae; use of high-speed nets appears to decrease avoidance.

Results of vertical distribution studies of two Atlantic species, yellowtail flounder and haddock, show that young larvae may have a different distribution than older larvae. The young larvae of both species did not migrate and remained below a thermal gradient; yellowtail flounder remained at 20-24 m, between the shallow and deep thermal gradients (Smith *et al.*, 1978), and haddock seemed to occur below the thermocline (Miller *et al.*, 1963). Older haddock (8-20 mm) did not migrate and appeared to be more abundant within the limits of the temperature discontinuity layer while older yellowtail flounder (4-10 mm) migrated as much as 15-34 m, crossing two separate 5° C thermal gradients. Ahlstrom (1959), on the other hand, found that the species he studied in the California Current did not move across the thermocline, a gradient of 4-8° C; offshore, larval Pacific mackerel and jack mackerel were observed in the upper 30 m and Pacific sardine and northern anchovy ranged deeper, to 50 m. The range in temperature where the majority of larvae were collected was restricted to 2° C for jack mackerel, 14-16° C; 3° C for northern anchovy and Pacific mackerel, 14-17° C; and 4° C for Pacific sardine, 13-17° C.

Current measurements by Smith *et al.* (1978) seemed to indicate that at night the yellowtail flounder larvae would be caught in the wind-driven surface layers, and during the day, at mid-depth, they would be transported in the opposite direction, resulting in relatively localized settling of the demersal stages.

An adaptive advantage of vertical migration for larval fish would be to accompany the diel migration of prey, and some larvae (Pacific hake, Sumida and Moser, 1980; cod, Ellertsen *et al.*, 1980) do show high post-sunset peaks in feeding incidence. But Smith *et al.* (1978) analyzed larval stomach contents and concluded that the daily movements of yellowtail flounder were not related to feeding.

Vertical migration may be an energy saving device. Northern anchovy (11 mm SL) that are below 10 m during the day migrate to the surface at night to fill their swim bladders; for larvae 13.5 mm and larger, the energy saved by using the swim bladder to maintain position in the water column at night exceeds the energy used to migrate to the surface (Hunter and Sanchez, 1976). Another advantage of these nightly migrations may be that they concentrate young larvae at the surface, thus increasing visual contacts that may facilitate schooling behaviour which begins at about 12 mm SL (Hewitt, 1980; Hunter, in press).

PREY

Size

The dimensions of prey organisms relative to larval fish mouth size are important variables which require consideration in any modelling effort. The size (usually measured at maximum width) of the prey eaten by fish larvae is a function of larval mouth width; within species mouth width is related to length, but mouth widths vary between species (Arthur, 1976; Beyer, 1980; Hunter and Kimbrell, 1980; Hunter, in press). For example, mouth width of northern anchovy and Pacific mackerel at first feeding is approximately the same size, 0.20 mm. But, between 5-15 mm SL, mouth width of Pacific mackerel rapidly increases in size; northern anchovy mouth also increases in size with age, yet at the same SL, northern anchovy mouth width averages about 30 percent smaller than Pacific mackerel width (Hunter, in press).

Although mouth width limits the maximum prey size, in nature fish larvae often do not eat maximum size prey. For example, at 14 mm Pacific mackerel have a mouth width of 1 mm; particles up to 0.8 mm are found in their guts, but the mean diameter of prey eaten by larvae in the sea was only 38 percent of their mouth width (i.e. 0.34 mm, Hunter and Kimbrell, 1980). Anchovy at the same standard length have a mouth width of 0.7 mm, and the maximum size prey observed in anchovy guts was 0.3 mm (Arthur, 1956; de Ciechomsky, 1967). Deviations are greater for hake larvae. Mouth width of 5 mm Pacific hake is 0.6 mm, and the mean width of prey eaten was about 0.08 mm, 13 percent of hake-mouth width (Sumida and Moser, 1980). Beyer's (1980) model of feeding success of clupeid fish larvae shows why optimum prey size, that allows the highest feeding success, is less than the maximum potential prey size determined from mouth measurements. However, there is a tendency for larvae in the sea to feed on progessively larger prey as they grow (Marak, 1960; Shelbourne, 1953; Rojas de Mendiola, 1974; Arthur, 1956). Furthermore, the dynamic population model of Jones and Hall (1974) postulates that cohorts of cod and haddock larvae must be spawned in the proper time to grow up with a cohort of their copepod prey (*Calanus sp.*).

In the laboratory it was found that size of prey fed to larvae must increase for larvae to grow at maximum rates. Small food particles (*Gymnodinium*; Table 3) sustained northern anchovy for more than two weeks, but growth was reduced (Lasker *et al.*, 1970). Feeding northern anchovy a larger particle (*Brachionus*) increased the growth rate (Theilacker and McMaster, 1971), however copepods were soon required for anchovy to attain maximum growth and survival through metamorphosis in the laboratory (Hunter, 1976). Hunter and Kimbrell (1980) described a similar increase in required particle size for rearing Pacific mackerel, as has Stepien (1976) for sea bream, Ware *et al.* (1980) for the anchoveta, *Engraulis ringens*, Jones *et al.* (1974) for turbot, *Scophthalmus maximus*, and Houde (1978) for three species of subtropical marine fish.

It should be stressed that both large- and small-mouth larvae eat small, more ubiquitous prey and that it is possible that fish larvae can eat enough small prey to meet metabolic demands for several days. This is the case with larval jack mackerel in the laboratory. Jack mackerel (large-mouth larvae) fed *Gymnodinium* from the onset of feeding (day 5) to age 12 days were the same size and as "healthy" (determined by histological assessment) as larvae eating *Gymnodinium*, *Brachionus*and copepods (Theilacker, unpubl.). However, northern anchovy fed on a *Gymnodinium* diet grew at maximum rate for three days only (Lasker *et al.*, 1970).

Beyer and Laurence (1980) conclude from their model of growth and mortality of larval herring that as larva reach certain sizes the energetic cost of each attack exceeds the gain from ingesting smaller food particles; this size depends upon the larva's metabolic requirements, which are both genetically and environmentally imposed.

Table 3. Prey size and caloric content.

Particle	Width (μm)	Dry wt. (μg)	Calories	Reference
Gymnodinium splendens naked dinoflagellate	50	-	0.00005	Hunter 1977
Brachionus plicatilis rotifer	133	0.16	.00085	Theilacker and McMaster 1971
Copepods[1]				
nauplii	200	0.80	.0042	Laurence 1977
nauplii	250	1.30	.0068	"
copepodid	600	15.40	.0809	"
nauplii		0.15		Houde and Schekter 1980
Artemia nauplii	236		.0096	Hunter 1977

[1] Copepod weight and fat varies seasonally causing caloric variations.

Selection

There is evidence for selection by food type. Gut analyses indicate that field-collected jack mackerel less than 10 days of age may select brightly coloured harpacticoid copepods (*Microsetella*, *Oncaea*, *Corycaeus*) (Arthur, 1976), and laboratory-reared jack mackerel may either be unable to catch or may reject *Labidocera* nauplii in favour of *Acartia* and *Paracalanus* (Devonald, pers. comm.). Although naupliar body size, .06-.09 mm diameter, of *Labidocera* and *Acartia* is similar, *Labidocera*'s appendages are 2-3 times longer than *Acartia*'s appendages; hence, *Labidocera* nauplii may be too large to ingest, or, owing to larger appendages, simply too fast to catch. However, most evidence points to selection related to particle size (Stepien, 1976; Uotani *et al.*, 1978; Hunter, in press). It is reasonable that larval fish exhibit little selectivity for food type; if food particles are rejected, selectivity costs energy. Something must be gained by being selective; selection of large food particles offers a gain, i.e. more calories ingested per energy expended (as particle diameter increases 2.5 times, calories increase by a factor of 10; Hunter, in press; Table 3). In the field, large-mouth larval Pacific hake, 3-8 mm contained large numbers of small organisms; however the large adult copepods that they ate accounted for 74 percent of the volume (hence, 74 percent of the calories) of food eaten (see table below, from Sumida and Moser, 1980).

	Range max.width (um)	Mean food volume ($10^6 um^3$)	Standard deviation (10^6 um^3)	Frequency	Frequency x volume (10^9 um^3)	% of total volume
Copepod eggs	50-100	0.364	0.083	674	0.24534	0.7
Copepod nauplii	40-300	4.013	5.148	441	1.76973	5.3
Copepodites	80-450	14.698	24.308	393	5.77631	17.4
Adult copepods	110-600	57.418	54.850	426	24.46007	73.8
Other	40-550	49.401	107.783	18	0.88922	2.7
					Σ = 33.14067	

Density

Critical prey density, the food concentration required for first-feeding larvae to initiate feeding, is a component of larval survival which has caused great controversy among scientists involved with larval fish research. Laboratory experiments to date have usually been done with somewhat uniform and high concentrations of prey and a relatively high density of larvae. Prior to 1970, threshold food-density experiments in the laboratory were considered "successful" when there was high survival and fast growth of larvae. Fishery biologists accepted that field-mortality rates in excess of 90 percent during the egg and larval stages produced healthy year-classes, but in the laboratory biologists demanded high survival rates. The critical prey densities determined by these experiments were higher than densities measured in the integrated natural larval habitats. Lowest survival rates in laboratory feeding experiments (Table 4) were usually at particle densities reported to be common in the field (Table 5); thus, these experiments may represent levels characteristic to the field. Houde's (1974; 1978) work on three species of subtropical fish reported significant survival at low prey densities; sea bream required 50 plankters/l and lined sole required 100/l (Table 4). These food levels are common in coastal and partly enclosed areas (Table 5; from Hunter, in press, and Houde, 1978).

Critical prey densities determined in the laboratory and presented in Table 4 are constant prey concentrations required for optimum survival from first feeding to 2-7 weeks of age (with the exception of the herring experiment that was conducted with older larvae). These densities vary among species and will also vary with life stages within species. For example, Laurence (1977) showed that the initial required prey density for winter flounder to meet metabolic requirements (including growth) was 800 nauplii/l; after successful feeding behaviour was established, the critical density decreased to 300 nauplii/l. Then as growth and metabolic demands increased, critical density increased to 600 nauplii/l. Laurence also showed that at the onset of feeding, winter flounder started feeding at 10 and 100 nauplii/l but did not survive longer than two weeks. Thus, threshold densities for first feeding (Table 4) are not indicative of particle concentrations required for survival during all life stages.

Laboratory experiments reveal that variations in prey density affect larval fish feeding rates, ration, activity, evacuation time, growth rates (time to metamorphosis), and gross growth efficiencies (Werner and Blaxter, 1980; Houde and Schekter, 1980; Wyatt, 1972; Laurence, 1977; Hunter and Thomas, 1974). Generally, as prey density increases, feeding rates, ration and growth rates increase (Table 6); gross growth efficiencies may increase or decrease (Table 9) and activity, evacuation time (Table 10) and time to metamorphosis decrease. Due to differences in experimental technique, comparisons of studies that depend on controlled prey levels need some qualifications. These restrictions are discussed in the final section of this review, wherein laboratory techniques and facilities for obtaining relevant physiological data are described, and comparative observations are tabled.

Table 4. Food density thresholds for 8 species of marine fish larvae

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density No./L	Survival at various food densities		Reference
					Density No./L	Percent survival	
PLAICE *Pleuronectes platessa* 5	5	14	*Artemia nauplii*	50 (larvae)	1,000	72[1]	Wyatt 1972
					500	72	
					200	54	
					100	32	
NORTHERN ANCHOVY *Engraulis mordax* 5	10.8	12	Wild zoo-plankton (nauplii)	10 (eggs)	4,000	51	O'Connell & Raymond 1970
					900	12	
					90	0.5	
					9	0	
BAY ANCHOVY *Anchoa mitichilli* 5	76	16	Wild zoo-plankton (nauplii-copepodites)[3]	0.5 - 2 (eggs)	.5,000	64	Houde 1978
					1,000	48	
					100	5	
					50	0-12	
SEA BREAM *Archosargus rhomboidalis* 5	76	16	"	0.5 - 2 (eggs)	500	72	" "
					100	37	
					50	13	
					25	7	
					10	4	
LINED SOLE *Achirus lineatus* 5	38	16	"	0.5 - 2 (eggs)	1,000	54	" "
					100	13	
					50	1	
HADDOCK *Melanogrammus aeglefinus* 5	37.8	42	Wild zoo-plankton (nauplii)	9[4] (larvae)	3,000	39	Laurence 1974
					1,000	22	
					500	3	
					100	0	
					10	0	
HERRING *Clupea harengus*	20	21-63 58-84	*Artemia*	8	3,000	4-8	Werner & Blaxter 1980
					1,000	3-12	
					300	0-8	
					100	0-12	
					30	0-1	
WINTER FLOUNDER *Pseudopleuronectes americanus*	64	49	Wild zoo-plankton (nauplii)	9[4] (larvae)	3,000	34	Laurence 1977
					1,000	4	
					500	3	
					100	1	
					10	0	

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[1] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).

[2] Estimated food density for indicated survival levels.

[3] Plankton blooms of Chlorella sp. and Anacystis sp. maintained in rearing tanks.

[4] Estimated by adjusting for hatching success.

5 Hunter, in press.

Table 5. Average[1] densities of microcopepods in the sea

	Average density of microcopepods (number per liter)				
	nauplii	copepodites	total	Location	Reference
OPEN SEA	13	2	15	Southeast Coast of Kyushu	Yokota *et al*. 1961
	22	36	58[2]	California Current	Beers and Stewart 1967
	40	5	45[2]	Southern California near shore	Beers and Stewart 1970
	27	7	34[3]	Eastern Tropical Pacific	Beers and Stewart 1971
	36	1	37	California Current	Arthur 1977
PARTLY CLOSED	76	19	95	Azov Sea	Duka 1969
	-	-	223[4]	Gulf of Taganrog	Mikhman 1969
	40	-	40	North Sea (0-10 m)	Ellertsen *et al*. 1980
	20-30	-	25	North Sea (10-20 m)	"

[1] Mean for all stations and years given in publication listed in table (Hunter, in press).

[2] Includes all copepods passing 202 µm mesh net.

[3] Includes all copepods passing 202 µm mesh net and caught on 35 µm mesh.

[4] Defined as food of *Clupeonella delicatula*; microcopepods account for over 90% of items eaten (Mikhman 1969).

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Reported concentrations of some potential larval fish food organisms from coastal and estuarine areas. (Table 10 from Houde 1978)

Reference	Place	Organisms	Concentration
Burdick (1969, cited in May, 1974)	Kaneohe Bay, Hawaii	copepod nauplii	50-100/1 common 200/1 sometimes present
Duka (1969)	Sea of Azov	*Acartia clausi* nauplii Other copepod nauplii and copepodids Total	62-65/1 > 30/1 > 90/1
Mikhman (1969)	Gulf of Taganrog, Sea of Azov	Early stages of copepoda	39-546/1
Hargrave and Green (1970)	Two eastern Canada estuaries	Copepod nauplii and copepodids	> 60/1
Reeve and Cosper (1973)	Card Sound, South Florida	Copepod stages 20-200 µm in breadth Tintinnids	range 23-209/1 mean for 28 collections 72/1 range 40-369/1
Heinle and Flemer (1975)	Patuxent River estuary	*Eurytemora affinis* nauplii & copepodids	>100/1 frequently >2,000/1 occasionally
Houde (unpublished data)	Biscayne Bay, South Florida	Copepod nauplii and copepodids <100 µm in breadth Tintinnids	usually 50-100/1 frequently >100/1

Table 6. Feeding rates at various prey concentration.

Species	°C	Age (d; mm; µg)	Container volume (liters)	Prey type	Prey concentration (#/l)	Feeding rate (#/h)	% body wt. eaten per day	Reference
YOUNG LARVAE								
Pacific sardine	16	first-feeding	500	nauplii^1	max.	2		Schumann 1965
Sardinops sagax	"	15-17 mm	"	*Artemia*	max.	60^2		
Northern anchovy^3	17	4 d; 20 µg	500	Rotifer^4	10,000-	15.0	144	Hunter 1972
Engraulis mordax	"	10 d; 70 µg	"	"	20,000	46.0	126	
Bigeye anchovy^6	26	2 d; 3.6 mm	9.5	nauplii$^{1-5}$	100	43.0	440	Chitty 1980
Anchoa lamprotaenia	"	8 d; 5.5 mm	"	"	"	70.0	197	
Bay anchovy^6	26-28	4 d; 4.8 µg	76	nauplii$^{1-5}$	50	0.5	20	Houde & Schekter 1980
Anchoa mitchilli	"	4 d; 13.4 µg	"	"	100	2.4	39	
	"	4 d; 17.4 µg	"	"	1000	19.3	221	
Sea bream^6	26-28	4 d; 13 µg	76	nauplii$^{1-5}$	50	0.9	21	Houde & Schekter 1980
Archosargus rhomboidalis	"	4 d; 12.7 µg	"	"	100	1.3	28	
	"	4 d; 18.2 µg	"	"	1000	9.0	158	
" "	23-26	2-3 d	75	nauplii$^{1-5}$	1000	8.0		Stepien 1976
	29	2-3 d	"	"	"	18.0	199	
" "	23	16 d	75	nauplii$^{1-5}$	1000	54.0		"
	26-29	16 d	"	"	"	150.0		
Pacific mackerel	19	3 d; 38 µg	200	Rotifers^4	157,000	14	70	Hunter and Kimbrell 1980
Scomber japonicus	"	4 d; 43 µg	"	"	47,000	20	89	
	"	5 d; 85 µg	"	"	198,000	45	102	
Striped knifejaw^7	22	7 d 3.9 mm	-	Rotifers	5,000	6		Fukusho 1979
Oplegnathus fasciatus	"	13 d; 5.2 mm	-	"	"	44		
Lined sole^6	26-28	4 d; 8.7 µg	76	nauplii$^{1-5}$	50	0.2	6	Houde & Schekter 1980
Achirus lineatus	"	4 d; 11.4 µg	"	"	100	1.1	21	
	"	4 d; 13.5 µg	"	"	1000	12.0	80	
Plaice	7			Rotifers		35		Howell 1973
Pleuronectes platessa								
OLDER LARVAE						Ration # food items/fish		
Herring^6								
Clupea harengus	9	4 wks.	20	*Artemia*	30	5		Werner and Blaxter 1980
					100	4.5		
					300	4		
					1000	6		
					3000	5		
" "	9	5 wks.	20	*Artemia*	30	6		"
					100	6		
					300	8		
					1000	8		
					3000	7		
						Ration (dry wt; µg)		
Winter flounder	8	2 wks.	64	nauplii^1	100	1		Laurence 1977
Pseudopleuronectes americanus					500	2		
					1000	1		
					3000	2		
" "	8	5 wks.	64		100	11		"
					500	19		
					1000	25		
					3000	23		

[1] wild plankton - copepod nauplii
[2] 3.5 strikes/min for 10 min until gut full; then 1/min
[3] estimated from number strikes and adjusted for percent successful capture
[4] dry wt = 0.16 µg (fresh material)
[5] dry wt = 0.15 µg (fresh material)
[6] larval dry wts determined for preserved samples
[7] hatch at 2.2 mm; gut length intermediate between Pacific mackerel and jack mackerel; growth rate begins at 0.2 mm/d and increases to 0.5 mm/d (similar to anchovy, Table 2).

Houde and Schekter (1980) compared feeding rates, ration and growth among three marine fish, bay anchovy, sea bream and lined sole, fed at several low but constant prey concentrations (Table 6). Feeding rates of the three species increased with increasing prey density; however, at the onset of feeding, the sea bream, a sparid, was more effective at capturing prey at the lowest density, 50 prey/l, than anchovy or sole. But, anchovy had the highest feeding capability at 50 and 100 prey/l after the first few feeding days when anchovy had increased their prey-capturing efficiency. Sea bream had the best potential to increase growth rates at higher food levels, 500-1 000/l, and were capable of higher survival at low prey densities, 100/l (37 percent survival) than anchovy or sole (5-13 percent survival; Table 4). Thus, although ration increased with increasing prey density, the feeding abilities of these three species, that differ in morphology and behaviour, varied at the different prey densities.

Feeding rates of older herring larvae (Werner and Blaxter, 1980) and older winter flounder (Laurence, 1977) fed at several prey levels also increased with increasing prey density until a maximum ration was achieved. This maximum ration was achieved in both cases at 1 000 prey/l. Growth rates within species were the same at prey densities from 300 to 3 000 prey/l, but were significantly less at 100/l. Laurence (1977) found that survival of winter flounder increased with increasing prey levels, but Werner and Blaxter (1980) did not find this with herring larvae. Perhaps, suitability of prey type was a factor affecting survival; winter flounder were eating copepods, a natural prey, and herring were eating *Artemia*.

In addition to depending on prey density, feeding rates also depend on life stage and temperature. A 3-6°C increase in temperature may triple feeding rates (Stepien, 1976), and a 5-6 day increase in age of young larvae raises feeding rate 2-7 times (Table 6).

At high prey densities of *Artemia* nauplii (5 000/l), herring larvae exhibited reduced ingestion of the prey; furthermore, the prey were evacuated faster from the stomach and were not complete digested or assimilated (Werner and Blaxter, 1980). Houde and Schekter (1980) also recorded a decrease in gross growth efficiency at the highest prey concentrations for the three species they tested (Table 9).

Distribution

One of the major questions arising from the evaluation of laboratory feeding experiments, such as those mentioned in the preceding sections, is where areas exist in the field with the necessary concentrations of esculent food for larval fish. The sampling gear most often employed (pumps and plankton nets) sample large volumes of water and gives results that average numbers of organisms over depths or distances. Despite these sampling difficulties, Lasker (1975) found natural occurrences of the high prey densities (20 000-40 000/ml) that are needed by northern anchovy to initiate feeding. The prey particles, a dinoflagellate, *Gymnodinium splendens*, occurred in water taken from the chlorophyll maximum layer. Similar bioassay experiments with cod larvae showed feeding at 30-40 nauplii/l. The maximum naupliar biomass was found at 0-15 m and 60-80 percent of the larvae sampled from these depths had 2-3 nauplii in their guts (Ellertson *et al.*, 1980). Owens (this volume), and Mackas (1976) have attempted to apply more sensitive and discrete sampling techniques. They have found microstratification of esculent food particles in appropriate numbers to support larval fish survival. Further use of these techniques should lead to more information on prey distribution on the scale relevant to a larval fish.

Vlymen (1977) used an empirically based mathematical model to demonstrate the importance of food microstructure (geometry) and behaviour, and how they affect growth of northern anchovy larvae. He found that the critical habitat of an anchovy larva should contain between 14 and 32 particles/ml. Within this range the numbers represent a structured environment with 14 particles/ml in the interpatch areas and 32 particles/ml in the critically dense regions of contagion.

Lasker and Zweifel (1978), using a modified version of Vlymen's model (1977) for northern anchovy larval growth, determined that "it is not the absolute concentration of the large particles that govern their capture by the larva, but rather their concentration relative to the larger number of small particles in the larval environment." In this simulation, large particles made very little contribution to survival when the immediate environment of the first-feeding larva contained 40 small particles/ml. Because it is more likely that there will be aggregations of small particles than large ones, survival of first-feeding larvae would be enhanced by a favourable number of patches of that density within their habitat.

In the laboratory, it has been shown that larval survival is increased by exposure to a food patch; however, larval behaviour to patch situations differ. Houde and Schekter (1978) found that during a 13 hour feeding day a short, 2-3 hour patch exposure increased survival of larval sea bream from 7.5 percent (on day 16) to 20 or 30 percent. On the other hand, bay anchovy larvae needed a 9 hour exposure for 10 percent survival. Thus, larval sea bream appear to be more capable of taking advantage of periodic patch conditions than bay anchovy.

LARVAL MODEL PARAMETERS AND REQUISITE LABORATORY RESEARCH

Existing larval survival models were developed from basic energetic principles based on laboratory and field studies. These models consist of conjectures concerning the manner in which excess energy (i.e. the difference between the energy expended in capturing and processing food and energy gained) results in growth and/or survival. Thus, basic physiological data are the bases for the models. In spite of the sophisticated mathematics of the models, the results can be worthless if the physiological data is gathered through inaccurate or biasing techniques. This discussion describes some parameters used in models and the techniques used to measure these parameters.

Rearing containers

Container size may be a critical variable in larval fish studies. Size of container affected results in jack mackerel rearing experiments; larvae grew faster and were in better nutritional condition in 100 l than in 10 l containers (Theilacker, 1980c). Size of container also affects swimming speed. For example, swimming speed of laboratory-held larval herring was less than *in situ* contained herring — 0.9 cm as compared to 1.59 cm (von Westernhagen and Rosenthal, 1980). Likewise, northern anchovy swim 3-4 times faster in large than in small containers (Hunter, pers. comm.; see Swimming speed).

Metabolic rates

The sensitivity of the techniques used to determine oxygen consumption is limited by experimental container volume. Volumes need to be small in the case where oxygen consumption rates are low and very small total changes are expected; hence fish larvae are definitely confined and movement is probably restricted. Experimentalists that use Warburg (10 ml) or Winkler (40-60 ml) techniques (Table 7) usually assume that the respiration estimates are somewhere between "resting" and "active". Vlymen (1974), in his estimate of swimming energetics of northern anchovy, suggested that activity in the confines of a small container would be inhibited and below natural levels. However, it has been shown that average respiration rates (determined by Warburg) of groups of early stage Pacific sardine eggs were the same as rates determined for single, late stage eggs housing "active" larvae (Lasker and Theilacker, 1962). Because fish eggs probably are not affected by restrictive containers, this observations shows that shaking Warburg flasks, required to equilibrate oxygen between water and air, may induce "active" metabolism.

Variation in "resting" (standard) metabolic rates among poikilotherm species can sometimes be explained by differences in experimental temperature. The temperature coefficient of respiration (Q_{10}, a measure of the increase in rate of an activity for a 10°C temperature difference) is typically about 2-4 (Giese, 1962). The Q_{10} of respiration for Pacific mackerel (at unknown activity) between 18° and 22°C is about 5 (Table 7). But, differences in metabolic rates between anchovy and mackerel (Table 7) cannot be explained by differences in temperature and must be caused by differences in activity and metabolic demands. Hence, knowledge of activity is needed to make meaningful comparisons of metabolic rates among species. Activity has been shown to increase respiration rates up to 3.5 times for Pacific sardine larvae (Lasker and Theilacker, 1962) and 5-10 times for larval herring (Holliday *et al.*, 1964).

Because activity increases respiration rates, extrapolations of laboratory-determined respiration rates to the field conditions are difficult due to our inability to accurately measure activity in the field. Ware (1975) suggests using a value of 2.5 times "standard" ("resting") metabolic rate to estimate "active" field metabolism. However one value will not likely account for interspecific differences in metabolic demands, i.e. such as differences in activity at first feeding of "beat" and "glide" swimmers like Pacific sardine and

Table 7. Respiration rates.

			ul/mg/hr						
			Egg			Larva			
Species	°C	Age (d; mm; µg)	Resting	Activity unknown	Active	Resting	Activity unknown	Active	Reference
Pacific sardine[1]	14	-	0.8		1.8				Lasker and
Sardinops sagax	14	1-2 d				1.3		2.7	Theilacker 1962
Northern anchovy[2 3]	17			1-1.5					Theilacker
Engraulis mordax	17	1-3 d					3.5		(unpubl.)
	17	4-30 d[4]					4.1(3.1-6.9)		
	17	15 mm; 30 d[5]					6.7		
Herring	8	1-10 d				2.3		10-23	Holliday *et al.*
Clupea harengus									1964
Pacific mackerel[3 6]	18	3.7-17.9 mm					6.1		Hunter and
Scomber japonicus		3.2-10.5 mm					11.4		Kimbrell 1980
Rockfish[6]									
Sebastes rhodochloris	11	Late		1.8					Moser 1967
Sebastes eos	11	Late		2.0					
Winter flounder[6]	5	7 d; 12 µg					5.5[7]		Laurence 1975
Pseudopleuronectes americanus	5	7 wk; 250 µg					4.8[7]		
	5	7 d; 12 µg					6.0[8](2.8-9.8)		
	5	7 wk; 250 µg					6.5[8](3.4-9.7)		
Pollack[3]	4	11-14 d; 90-120 µg				1.4- 3.0			Clarke
Theragra chalcogramma									(pers. comm.)
Striped bass[6]	18	0 d		7.5					Eldridge
Morone saxatilis		5 d					5.4[7]		(pers. comm.)
		10 d					4.6		
		15 d					4.2		

[1] determined for individual eggs and larvae
[2] Winklers; 40-60 ml
[3] weight-specific rates; slope = 1
[4] N = 43
[5] 230 ml, no agitation; n = 2
[6] Warburgs; <10 ml
[7] weight-specific rates decreased; these rates taken from weight-specific metabolism regression
[8] median rates taken from actual data points and range

northern anchovy that rest 50-60 percent of the time (Schumann, 1965; Hunter, 1972) and the continuous swimming Pacific mackerel and jack mackerel (Hunter and Kimbrell, 1980; Theilacker, unpubl.). These species-specific behaviours point to large differences in required calories at the onset of feeding.

Growth

A comparison of laboratory growth of the California Current species illustrates species-specific differences in growth rates (Figure 1; Table 8). At similar temperatures, Pacific mackerel reach metamorphosis twice as fast as Pacific sardine and northern anchovy. Sardine and anchovy reach metamorphosis at about the same size, but initially larval sardines grow faster than larval anchovies, hence sardines reach metamorphosis at an earlier age. Growth rates of larval jack mackerel are slow; although jack mackerel transform at the same size and probably similar weight as Pacific mackerel, metamorphosis occurs about two weeks later than in Pacific mackerel. Zweifel and Lasker (1976) have shown that the Laird-Gompertz growth function may be used to define the genetically determined and dynamically changing growth rates in the early life stages of many fish.

Measuring changes in length is convenient for estimating growth, but it has been shown that shrinkage in length of laboratory-preserved larvae differs from shrinkage of field-collected larvae (Theilacker, 1980b); hence, to compare animals at the same developmental stage there is a need to intercalibrate laboratory and field measurements. For northern anchovy larvae, difference in shrinkage between laboratory-preserved larvae (pipetted directly into Formalin) and netted and preserved larvae (simulated field-collected) of the same initial size decreased with age. For example, 3 mm larvae that were netted and preserved in Formalin shrank 15 percent more than 3 mm larvae that were laboratory preserved, but shrinkage of 20 mm larvae was the same for both treatments (Theilacker, 1980b). Thus, for estimates of larval growth, shrinkage calibration is important for small larvae. Shrinkage appears to be species specific; shrinkage of body parts is not the same among larvae with similar body forms (e.g. compare mackerels in table below).

	Laboratory formalin			10 min. net treatment			Formalin preservation after net treatment		
	SL	HL	BD	SL	HL	BD	SL	HL	BD
Northern anchovy	.92	.91	.90	.81	.91	.70	.78	.88	.67
Jack mackerel	.92	.91	.80	.90	.91	.84	.87	.88	.81
Pacific mackerel	.92	--	--	.90	.90	.98	.86	.86	.94

Ratio = treated size/live size; 1.00 = no shrinkage
-- = no data
SL = standard length; HL = head length; BD = body depth measured at anus

A better estimate of growth than the change in larval length is the change in dry weight. Measuring changes in dry weight allows estimates of energy incorporated during growth and is more suitable for interspecific comparisons of growth. For example, at 20 days of age, northern anchovy raised at 17°C and Pacific mackerel raised at 16.8°C are about the same length, 10 mm SL, but their weights differ by a factor of 6, anchovy weigh 0.3 mg and mackerel 1.9 mg (Hunter, in press). Thus, feeding of Pacific mackerel during this 2-3 week period must be more intense and/or the size of the food eaten must be greater (hence more calories/food item) than food eaten by northern anchovy.

Table 8. Growth.

		Growth rate (mm/d)					Metamorphosis			1 year	
		Days									
Species	°C	4-15[1]	16-30	31-40	41-50	Reference	Size (mm SL)	Age (days)	Reference	Size (mm SL)	Reference
Pacific sardine, *Sardinops sagax*	16-19	1.0	0.5	0.5	0.5	(4)	31-35	45-50	(4) (8)	120	(8)
Northern anchovy, *Engraulis mordax*	17	0.2	0.5	0.5	0.5	(5)	34-40	50-60 90	(9) (11)	95-115[2]	(11)
Jack mackerel[3], *Trachurus symmetricus*	15	0.1	0.2	0.5	1.0	(6)	11-16	40	(10)	200	(12)
Pacific mackerel, *Scomber japonicus*	16.8	0.1	1.0	-	-	(7)	15	25	(7)	272	(13)

[1] Hatching = day 0

[2] Size at 1 year = 115 mm at low anchovy biomass; high-biomass size = 95 mm

[3] Large-egg larvae

[4] Kimura 1970

[5] Kramer and Zweifel 1970

[6] Theilacker 1978

[7] Hunter and Krimbrell 1980

[8] Ahlstrom 1966

[9] Hunter 1976; lab

[10] Ahlstrom and Ball 1954; Theilacker (unpubl.)

[11] Methot (pers. comm.); field, age estimated from daily otolith increments

[12] Wine and Knaggs 1975

[13] Knaggs and Parrish 1973

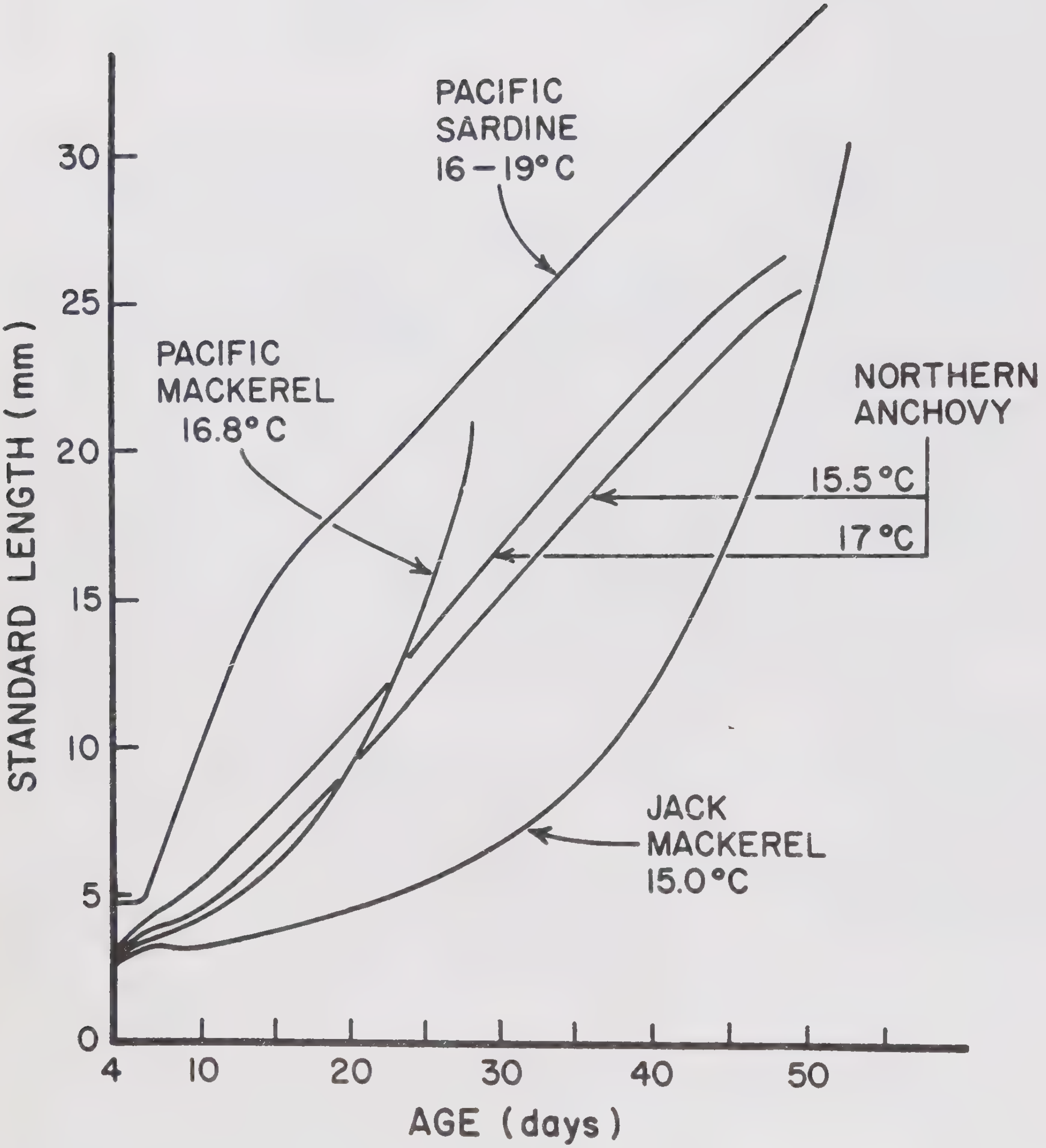

Figure 1. LABORATORY REARED FISH

It is important that dry weights be determined with fresh samples. Formalin perservation caused a 30 percent decrease in dry weight of larval sardines, and preservation in ethyl alcohol decreased dry weights of Pacific mackerel by 50 percent (30-80 percent) (Theilacker, unpubl.). These determinations were for young, 4-6 mm SL larvae. Methot (pers. comm.) weighed field-collected, alcohol-preserved anchovy to determine weight at age, estimated by increase in otolith increments. His weights for 15-30 mm SL larvae were 30-40 percent less than the fresh dry weights determined by Hunter (1977). Thus, weight loss in alcohol preservative does not appear to decrease with increasing larval size.

Laurence (1978) measured unpreserved dry weights for seven species of larval fish common to the American east coast. He presented his data as linear regressions, $\log_{10}$ weight on $\log_{10}$ length. The species were from different taxonomic families (Clupeidae, Gadidae, Sparidae, Bothidae and Pleuronectidae) but there were no obvious species-specific correlations with the length-weight regressions. The length exponents ranged between 3.78-4.77 and averaged 4.15, thus weight was proportional to length to the fourth power. Length-weight relations for northern anchovy and Pacific mackerel are curvilinear (Hunter, 1976; Hunter and Kimbrell, 1980), therefore extrapolations of linear regressions of length-weight measurements are probably inappropriate.

Prey density

Because variations in prey density affect larval fish feeding rates, ration, activity, evacuation time, growth rates, and gross growth efficiencies, accurate estimates of prey levels are needed for comparisons of experimental results. Many young larvae are delicate, and extremely susceptable to mechanical injury; thus, experimental rearing containers are not mixed to randomize prey distribution until larvae are older. As a result, in experiments that control prey levels, the effective density available to larvae must vary; at low prey levels, food patches may form and thereby elevate the actual density of food encountered by some larvae. In addition, some larval rearing techniques include use of high algal concentrations ("green" water) in rearing containers with invertebrate prey and fish larvae (Stepien, 1976; Houde and Schekter, 1980). In these experiments, it is difficult to assess whether consumed algae directly provided calories to fish in addition to the prey calories; this is particularly important at low prey levels. Inter-experimental comparisons of life functions that may be affected by prey concentration and media differences (i.e. algal content) are difficult and lead to uncertainties regarding their general comparability.

Growth efficiencies

Because it is presently impossible to accurately measure metabolic rates during various swimming and feeding behaviours and to describe behaviour and activity in the field, a comparison of interspecific growth efficiencies may elucidate those species that maximize their growth relative to others in similar environments and feeding regimes. A high growth efficiency (calories of growth/calories consumed) indicates efficient assimilation of food energy for growth, with little being lost by excretion or used in respiration, thus conservative expenditure of energy for swimming and feeding. Calories of growth can be estimated from daily increases in dry weight, and calories consumed can be estimated from the daily ration. Meaningful estimates of growth calories depend on whether energy expenditure for swimming and feeding is the same in the laboratory and the field. Laboratory and field age-length measurements are also needed.

Procedures used to estimate ration (calories consumed) for larval fish vary. Ration has been estimated by (1) feeding rate x weight of prey x hours feeding (Houde and Schekter, 1980; Stepien, 1976), (2) weight of stomach at capture x hours feeding/hours to clear gut (Laurence, 1977), or (3) weight of mean stomach contents x gastric evacuation rate x hours feeding + weight of mean stomach contents (Hunter and Kimbrell, 1980). Daily ration estimates in percent of body weight eaten per day range from 70-300 percent for larvae fed 1 000 or more prey/l (Table 9).

Table 9. Gross growth efficiencies.

	°C	Age (d; µg)	Prey density (#/L)	Container volume (liters)	Daily ration		Gross efficiency (%)	Reference
					ug	% body wt.		
Bay anchovy[1]	26	17 d; 200 µg	50	10	19	31	57	Houde & Schekter 1980
Anchoa mitchilli	"	15 d; 200 µg	100		37	51	32	
	"	11 d; 200 µg	1000 nauplii (wild plankton)		115	140	14	
Herring *Clupea harengus pallasi*	-	12-22 d; 100-150 µg	14,000-20,000 rotifers	8			71	Eldridge *et al*. 1977
Sea bream[1]	26	17 d; 200 µg	50	10	12	-	83	Houde & Schekter 1980
Archosargus rhomboidalis	"	15 d; 200 µg	100		31	42	38	
	"	10 d; 200 µg	500 nauplii (wild)		45	-	38	
" "	23-26	2-3 d	1000	75	14	68-147	33	Stepien 1976
	29	2-3 d	1000		32	199	16	
	23	10 d	1000		-	69	31	
Pacific mackerel[2]	19	3 d; 38 µg	157,000	200	27	70	20	Hunter & Kimbrell 1980
Scomber japonicus	"	4 d; 43 µg	47,000		38	89	37	
	"	5 d; 85 µg	198,000 rotifers		86	102	44	
Striped bass	18	15 d; 400 µg	10				13	Eldridge (unpubl.)
Marona saxatilis	"		100				15	
	"		500				20	
	"		1000				21	
	"		5000 *Artemia*				50	
	18	29 d	10				20	
	"		100				14	
	"		500				17	
	"		1000				19	
	"		5000 *Artemia*				32	
Lined sole	26	21 d; 200 µg	50	10	14	-	63	Houde & Schekter 1980
Achirus lineatus	"	17 d; 200 µg	100		20	29	52	
	"	12 d; 200 µg	1000 nauplii (wild)		74	~90	20	
Winter flounder[3,4]	8	2 wks.	500				10	Laurence 1977
Pseudopleuronectes americanus	8	7 wks.					20	
	8	2 wks.	nauplii-copepods			300	15	
	8	7 wks.	3000			30	33	

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[1] Daily ration estimated from grazing experiments; dry weights determined with preserved larvae; wild plankton nauplii 0.15 ug, fresh dry wt.

[2] Ration from stomach contents and evacuation rate (discontinuous feeding).

[3] Ration from stomach contents and evacuation rate (active feeding).

[4] Net growth efficiencies.

Gut clearance times depend on feeding history; the time to a clear gut depends on the amount of food in the stomach (Werner and Blaxter, 1980) and it is more rapid at high food densities. Hence, gut clearance rates should probably be estimated from actively-feeding larvae. The technique used to avoid evacuation-time biases that may occur from discontinuous feeding (transferringlarvae with full guts into tanks without food and subsequently noting the time taken to evacuate gut contents), is first to present larvae with natural prey to fill guts and then with dyed prey and note time to first dyed fecal material. Most experimentally-determined evacuation times (Table 10) are for discontinuous feeding.

From Table 10, the observed evacuation times ranged from 3-9 hours; time decreased with (1) increasing prey density (herring, Werner and Blaxter, 1980), (2) age (knifejaw, Fukusho, 1979; Pacific sardine, Arthur, 1956), and (3) temperature (herring, Blaxter, 1965; Table 9). Larvae of two *Anchoa* species (Chitty, 1980) deviate greatly from the "average", having evacuation times measured in minutes, 7-13, instead of hours. Schumann (1965) also noted a fast time, 3 minutes, for anchovy larvae fed *Artemia* nauplii to form a food plug at the anus in 15 mm northern anchovy (Table 10).

Some fish larvae are more capable of digesting certain prey types than other fish larvae. Although *Artemia* nauplii allow survival of herring and plaice, *Artemia* are an inferior food for northern anchovy; anchovy do not appear to digest *Artemia* until after gut differentiation (Hunter, 1976). Jack mackerel also may be unable to digest Artemia; mackerel defecate profusely when fed a diet of *Artemia* (Theilacker, unpubl.).

Gross growth efficiencies are not dependent on digestive efficiencies. Only Laurence's (1977) growth estimates in Table 9 are for net efficiency (assimilated calories/calories consumed); he assumed the coefficient of utilization to be 0.7.

It is well known that growth efficiencies of the young are higher than in older animals. Efficiency of yolk utilization (conversion of yolk to tissues) of fish embryos ranges between 50-79 percent (Pacific sardine 79 percent, Lasker, 1962; herring 50-74 percent, Blaxter and Hempel, 1966; herring 74 percent, Eldridge *et al.*, 1977). Growth efficiencies for exogenous feeding, on food not as well suited for assimilation as yolk, are lower (Table 9). Results from the few measurements of larval growth efficiencies in Table 9 are inconsistent. Efficiencies apparently decrease with (1) increasing prey density (Houde and Schekter, 1980), (2) age (Eldridge, unpubl.), and (3) increasing temperature (Stepien, 1976); apparent efficiencies may also increase with (1) increasing prey density (Laurence, 1977; Eldridge, unpubl.) and (2) age (Hunter and Kimbrell, 1980; Laurence, 1977). As a result, it is impractical to try to make interspecific comparisons.

The growth efficiencies for larvae fed 1 000 or more prey/l are fairly high, 14-41 percent. It seems reasonable that most of the food energy would be used in growth in larval fish. Faster growing individuals develop more quickly, hence rapidly growing larvae will become faster swimmers and more able to avoid predators at an earlier age.

Temperature

Many abiotic factors (temperature, light, salinity, currents) may influence growth of fish larvae. Because temperature is relatively easy to measure, there is more information on effects of temperature than on other factors. Temperature may affect larval fish by influencing (1) oxygen content of sea water, (2) nutrients that control algal blooms, (3) time, place and duration of spawning, (4) incubation time, (5) size at hatching, (6) efficiency of yolk utilization, (7) growth, feeding rates and time to metamorphosis, (8) behaviour and swimming speed, (9) digestion and evacuation, (10) metabolic demand, and (11) distribution (Table 11). Thus, in laboratory experiments designed to test any of the above eleven parameters, temperature must be rigidly controlled.

Table10. Evacuation; time to empty gut.

	°C	Age (d; mm; µg)	Prey density (#/L)	Time to fill gut (hr)	Time to empty gut (hr)	Reference
Pacific sardine *Sardinops sagax*	- - -	5.5 mm 6-9.5 mm 10-25 mm	field " "	0.15[1] - -	11 6 3	Arthur 1956
Herring[2] *Clupea harengus*	9	3-9 wks.	3,000- 30,000 *Artemia*	1-3	3-4	Werner & Blaxter 1980
	"	3-9 wks.	30-300 *Artemia*	-	7+[3]	
" "	7	12d; 9 mm	-	-	8	Blaxter 1965
	15	12 d; 9 mm	-	-	4	
Northern anchovy *Engraulis mordax*	17	4-5 d	20,000 rotifers;	0.5	- 5-6	Hunter 1972 Moffatt, pers. comm.
	17	15 mm	*Artemia*;	-	<.05[4]	Schumann 1965
			field		1-3	Arthur 1956
Big eye anchovy[2] *Anchoa lamprotaenia*	26	2 d 8 d	100[6] nauplii	0.1[5]	0.15[4] 0.12[4]	Chitty 1980
Bay anchovy[2] *Anchoa mitchilli*	26	2 d 8 d	100[6] nauplii	- -	0.22[4] 0.18[4]	Chitty 1980
Whitefish[7] *Corygonus clupeaformis*	14	19-20 mm	max[6]; nauplii	-	16 ½ in 6	Hoagman 1974
Striped knifejaw[7] *Oplegnathus fasciatus*	22	7-11 d; 3-4 mm	4,000- 10,000 rotifers	0.5	6.5-9.4	Fukusho 1979
	"	13-18 d; 5-8 mm		-	2-2.5	
Pacific mackerel[7] *Scomber japonicus*	19	3-5 d	30,000 rotifers	<1.0	½ in 2	Hunter & Kimbrell 1980
Pacific hake *Merluccius productus*	-	3-11 mm	field	-	~11	Sumida & Moser 1980
Plaice *Pleuronectes platessa*	-	-	field	3	6	Ryland 1964
Winter flounder[2] *Pseudopleuronectes americanus*	8	-	1,000- 2,000[6] nauplii	-	6.6	Laurence 1977

[1] Schumann 1965; 15 mm; *Artemia*
[2] evacuation determined during active feeding
[3] complete digestion; little-no evacuation
[4] incomplete digestion
[5] to 50% fullness
[6] wild plankton-copepod nauplii
[7] evacuation determined during discontinuous feeding

Table 11. Effect of temperature.

HATCHING TIME	1)	At 13° Northern anchovy hatch about 1 day earlier than Pacific sardine	Lasker 1964
	2)	Pacific sardine do not develop normally below 13°C	Lasker 1964
	3)	Pacific mackerel do not hatch below 14°C	Hunter & Kimbrell 1980
HATCHING SIZE	4)	Herring; decreases with increasing temperature	Blaxter & Hempel 1963
	5)	Pacific sardine and Northern anchovy; no temperature effect	Lasker 1964
DEVELOPMENT: YOLK-SAC STAGE	6)	Pacific sardine; Q_{10}[1] = 4 for yolk absorption, and development of pigmented eyes and functional jaw (14-21°C)	Lasker 1964
EFFICIENCY OF YOLK ABSORPTION	7)	Plaice; more efficient at 6.5° than at 8.0°C; larvae 10% larger	Ryland & Nichols 1967
TIME TO EXOGENOUS FEEDING (FROM SPAWNING AT 15°C)	8)	Pacific sardine; 8 d	Lasker 1964
		Northern anchovy; 6-7 d	
		Jack mackerel; 8-9 d	Theilacker (unpubl.)
		Pacific mackerel; 7 d	
POINT OF NO RETURN (TABLE 1)	9)	Time to starvation decreases with increasing temp.	
FEEDING RATES (TABLE 6)	10)	Northern anchovy; 6-12 d, 6° (13-16°C) increased rate 4 times (<2 → 8 acts/min)	Hunter (in press)
	11)	Sea bream; 16 d, 3° (26-29°C) increased rate 2 times (8 → 18 acts/h)	Stepein 1976
GROWTH	12)	Pacific mackerel, 17-22°C; 7-15 mm; $Q_{10} = 3$ no effect of temp. 12 d	Hunter & Kimbrell 1980
	13)	Northern anchovy; 17-22°; 7-15 mm; $Q_{10} = 2.7$	Kramer & Zweifel 1970
ACTIVITY (TABLE 2)	14)	Northern anchovy, 6-12 d, 4° increase (13-17°C) increased swimming speed 2 times (0.4 → 0.9 BL/s)	Hunter (in press)
RESPIRATION RATES (TABLE 7)	15)	Pacific mackerel, 18-22°C; $Q_{10} = 4.8$	Hunter & Kimbrell 1980
	16)	Herring; $Q_{10} = 2$	Holliday, et al. 1964
GROSS GROWTH EFFICIENICES (TABLE 9)	17)	Sea bream, 2-3 d, 3-6° increase (23-26 to 29°C) decreased K; 33% to 16%	Stepein 1976

[1] $\log Q_{10} = \frac{10}{t_2 - t_1} \log \frac{k_2}{k_1}$

Responses to the same temperature may differ among species (Table 11). For California Current species at 15°C, time to the onset of feeding from spawning is earliest in northern anchovy, 6-7 days, and latest in jack mackerel, 8-9 days; at 15°C, northern anchovy can withstand starvation one day longer than Pacific mackerel and two days longer than jack mackerel. Northern anchovy have a greater tolerance for cooler temperatures than Pacific mackerel or Pacific sardine; anchovy will hatch and develop at 11°C, sardine do not develop below 12°C, and Pacific mackerel will not hatch below 14°C. Miscellaneous temperature responses are outlined in Table 11.

In conclusion, it is hoped that this information on the species-specific behavioural and physiological characteristics of fish larvae may lead to the identification of critical factors needed to predict larval fish survival. This summary of physiological laboratory research and field behaviour describes differences among fish species in spawning times, resistance to starvation, feeding rates, growth rates, feeding behaviour, swimming activity, and metabolic demands. Monitoring methods and models designed to predict larval fish survival must incorporate these species-specific functions. Clearly, more comparable standardized research techniques need to be used in producing descriptions of early life histories, and far more behavioural observations are needed to fully elucidate the diverse groups of larvae.

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Observations of a newborn Ross seal pup (*Ommatophoca rossi*) near the Antarctic Peninsula

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A Ross seal mother and male pup (*Ommatophoca rossi*) were sighted on 14 November 1978 in Dallmann Bay near the Antarctic Peninsula. This is believed to be the first documented observation of a newborn Ross seal. Behavioral observations and standard measurements taken from this pup enhance the small amount of information known about the early life of the species.

THOMAS, J., D. DEMASTER, S. STONE et D. ANDRIASHEK. 1980. Observations of a newborn Ross seal pup (*Ommatophoca rossi*) near the Antarctic Peninsula. Can. J. Zool. **58**: 2156–2158.

Une mère phoque *Ommatophoca rossi* et son petit, un mâle, ont été vus le 14 novembre 1978 dans la baie Dallman, près de la péninsule Antarctique. Il s'agit là de la première observation certaine d'un phoque nouveau-né de cette espèce. Des observations sur le comportement et des mesures étalons de ce petit viennent s'ajouter au peu d'information que nous possédions de la vie des petits de cette espèce.

[Traduit par le journal]

Introduction

On 14 November 1978 from aboard the United States National Science Foundation's Research Vessel *Hero*, a Ross seal pup (*Ommatophoca rossi*) was sighted in six octas of pack ice in Dallmann Bay (latitude 64°21.5′ S, longitude 62°47.4′ W). The only other documented observations of Ross seal pups are those of Solyanik (1964), who reported a female and pup on the South Sandwich Islands (latitude 56°00′ S, longitude 26°30′ W) on 6 December 1950, and Tikhomirov (1975), who collected eight females and their pups about 96 km south of the Scott Islands (latitude 67°24′ S, longitude 179°55′ W) between 18 and 21 November 1968. All of these animals were of unknown age, although Tikhomirov (1975) estimated the pups to be between 5 and 15 days old. The earliest reported fetal collection was on 23 September 1964 by Øritsland (1970). Six additional fetuses were collected by Øritsland near the South Orkney Islands (latitude 60°35′ S, longitude 45°30′ W) from 3 to 29 October 1964.

Materials and methods

The Ross seal mother and pup were observed under good visibility with binoculars from the crow's nest and pilot house for 30 min as the ship worked through the pack ice to their floe. We approached the final distance in a small boat and disembarked on the approximately 10 m by 10 m floe. The mother was restrained with a bag pulled over her head and foreflippers (Stirling 1966). Standard measurements and a series of photographs were taken of both seals, and the pup was weighed. Both seals received rear flipper tags.

When the female was unbagged, she left the floe, and was not seen again. We returned to the ship, and after cruising in the area searching for other seals, the floe was relocated 90 min later. The mother was not present. The pup was collected from brash ice beside the original floe, and the entire pup and the afterbirth on the floe were preserved in 10% formalin. Standard measurements (Table 1) were checked on this specimen, as described by Scheffer (1967). The pup is now deposited in the Smithsonian Institution, Washington, D. C. (specimen No. 504907).

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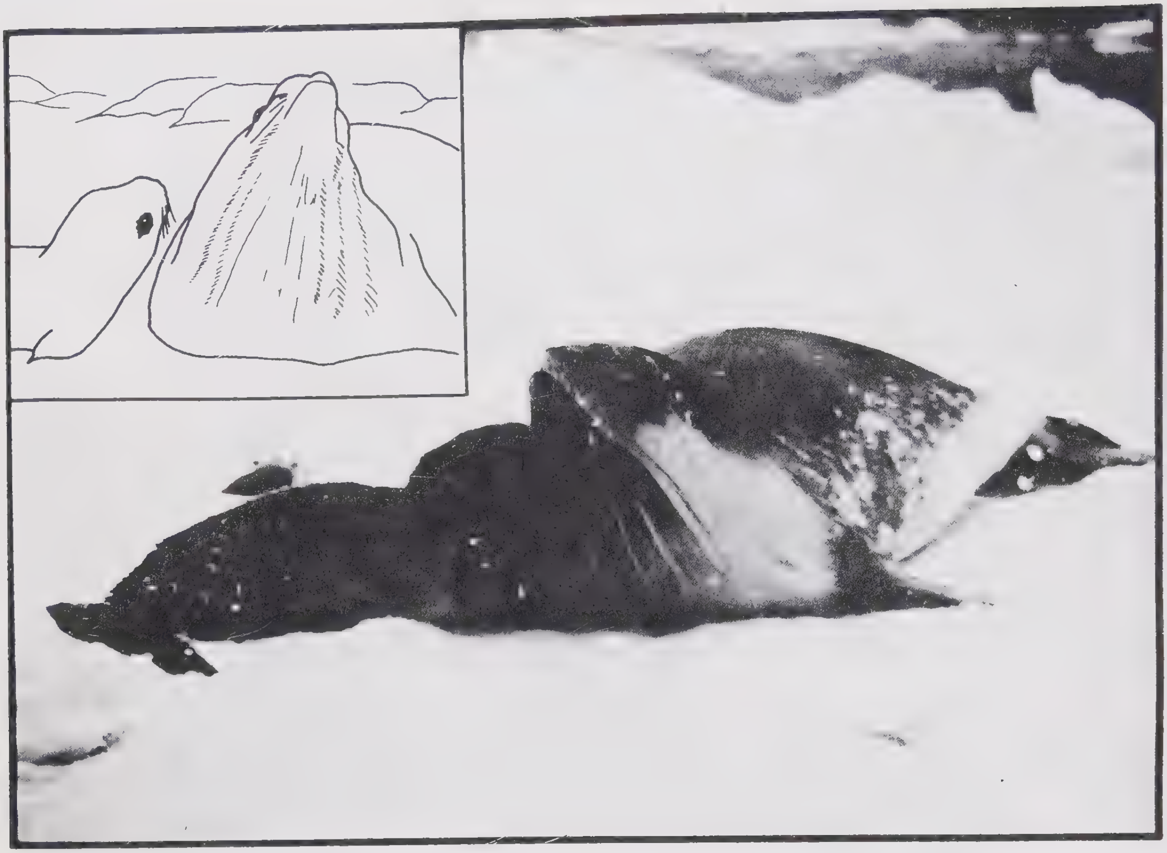

FIG. 1. Female and pup Ross seal (*Ommatophoca rossi*) showing striped throat pattern of both and afterbirth behind pup. Insert (from another photo) characterizes head-up posture of Ross seals.

TABLE 1. Summary of body measurements of a newborn Ross seal pup

Condylobasal length	17.8 cm
Zygomatic width	15.2 cm
Neck girth	41.9 cm
Axillary girth	55.9 cm
Standard length (nose to tail, direct)	96.5 cm
Nose–hind flipper length (direct)	116.8 cm
Live weight	16.8 kg

Results and discussion

This is believed to be the first observation of a newborn Ross seal. We believe that the pup was newborn because of the dampness of the lanugo, the presence of a soft, bleeding, 4-cm-long umbilical stump, and an unfrozen afterbirth which was not yet eaten by circling seabirds (Fig. 1).

The upper and lower canines and incisors were visible, but not erupted. Nails were obvious on both front and rear flippers. The lanugo pelage was generally dark on the dorsal body surface, light on the ventral surface, and exhibited a striping pattern on the throat similar to the adult pelage (Fig. 1).

The pup appeared precocious. He exhibited the characteristic head-up "singing" posture of the adults (Hofman et al. 1973). Actual suckling was not observed, but the pup gave bawl vocalizations and readily crawled around the floe. Twice we watched the pup move to an adjacent floe, through brash ice, which necessitated coordinated swimming, closing of the nares, and total submergence of the body.

The male pup weighed 16.8 kg, which was markedly lower than the weights of 40 to 75 kg reported by Tikhomirov (1975) and the predicted newborn weight of 27 kg made by King (1969). Table 1 shows body measurements collected from this pup. The mother's length was 188 cm.

October fetal lengths reported by Øritsland (1970) varied from 90 to 100 cm, with the September 23rd fetus measuring 101 cm in length. King (1969) estimated the newborn Ross seal length at 120 cm. The standard length of pups taken in November varied between 109 and 138 cm (Tikhomirov 1975). The mid-November length of this newborn Ross seal pup was 96.5 cm, which is less than that predicted by King (1969), but is intermediate between Øritsland's (1970) and Tikhomirov's (1975) findings. These measurements were taken about 16 days after the latest fetal collection made by Øritsland (1970). Therefore, this record of a newborn Ross seal pup supports Tikhomirov's assignment of the peak of pupping as sometime between 3 and 18 November.

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8088

BIOLOGY, DISTRIBUTION, AND ESTIMATES OF APPARENT ABUNDANCE OF THE SPINY LOBSTER, *PANULIRUS MARGINATUS* (QUOY AND GAIMARD), IN WATERS OF THE NORTHWESTERN HAWAIIAN ISLANDS:

PART II. SIZE DISTRIBUTION, LEGAL TO SUBLEGAL RATIO, SEX RATIO, REPRODUCTIVE CYCLE, AND MORPHOMETRIC CHARACTERISTICS

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ABSTRACT

Population structure in terms of size, legal to sublegal ratio, sex ratio, and reproductive cycle is defined for the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Trapping operations were conducted in waters of the Northwestern Hawaiian Islands from October 1976 to November 1978. Striking differences were noted in average sizes of lobsters among the various islands and banks surveyed. At Necker Island, where catch rates were estimated to be the highest in the island chain, the average sizes of males and females were the smallest. The proportion of legal lobsters in the catch was relatively high in most areas and males usually predominated. Egg bearing among females showed marked seasonality with peaks in early summer and fall. The length-weight relationship showed that, up to the 65-mm carapace length, males usually weighed more than females, but beyond this size females were heavier than males of equivalent sizes. Future research will be directed toward collection of data to define the reproductive cycle.

Northwestern Hawaiian Islands
spiny lobster
population structure
morphometric

INTRODUCTION

This report deals with studies on several aspects of the biology of the spiny lobster, Panulirus marginatus, caught in waters of the Northwestern Hawaiian Islands (NWHI) between October 1976 to November 1978. It represents an expansion of the preliminary analyses of data collected on P. marginatus by the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS) (see papers by Honda; Polovina and Tagami; and Uchida et al., part I).

METHODS

All data used in this study were collected during lobster and fish trapping operations on cruises of the NOAA ship Townsend Cromwell, TC-76-06, TC-77-02, TC-77-03, TC-78-01, TC-78-03, and TC-78-04 and on NMFS-chartered cruises of the RV Easy Rider, ER-77-02, parts I and II. The gear used--California two-chambered lobster pot and Hawaiian fish trap--has been described in Uchida and Hida (1977). The locations of the islands and banks are given in a separate paper (see paper by Uchida et al., part I).

The carapace length (CL), measured with a vernier caliper to the nearest 0.1 mm, is the distance along the mid-dorsal line from the transverse ridge between the supraorbital spines to the posterior margin of the carapace (McGinnis, 1972). All weights collected at sea were made on a beam scale to the nearest 10 g. Weights collected at the laboratory were recorded to the nearest whole gram using a single-pan balance. Tail weights were recorded when fresh (while at sea), and in the frozen and thawed states (on land).

RESULTS

Size distribution

The percentage frequency distribution of CL of male and female spiny lobsters caught during the surveys conducted from October 1976 to November 1978 are given by island and bank in Figure 1. The distributions are composites of all cruises and the data are grouped into 5-mm CL classes. Particularly striking are the differences in the means and variances of the size-frequency distributions among islands and banks and between sexes (Table 1).

The size-frequency distributions demonstrate that among all the areas sampled, the average sizes of the male and female lobsters at Necker were the smallest followed closely by those caught at French Frigate Shoals (Figure 1). At Necker, the relatively small size was evident even in October-November 1976 when our surveys first began and, therefore, does not represent a gradual reduction in size associated with increasing fishing effort and removal of the large dominant adults (Table 2).

The scarcity of juvenile lobsters smaller than 45 mm in CL suggests that they either occur in a different habitat or display different behavioral traits which affect their catchability. McGinnis (1972)

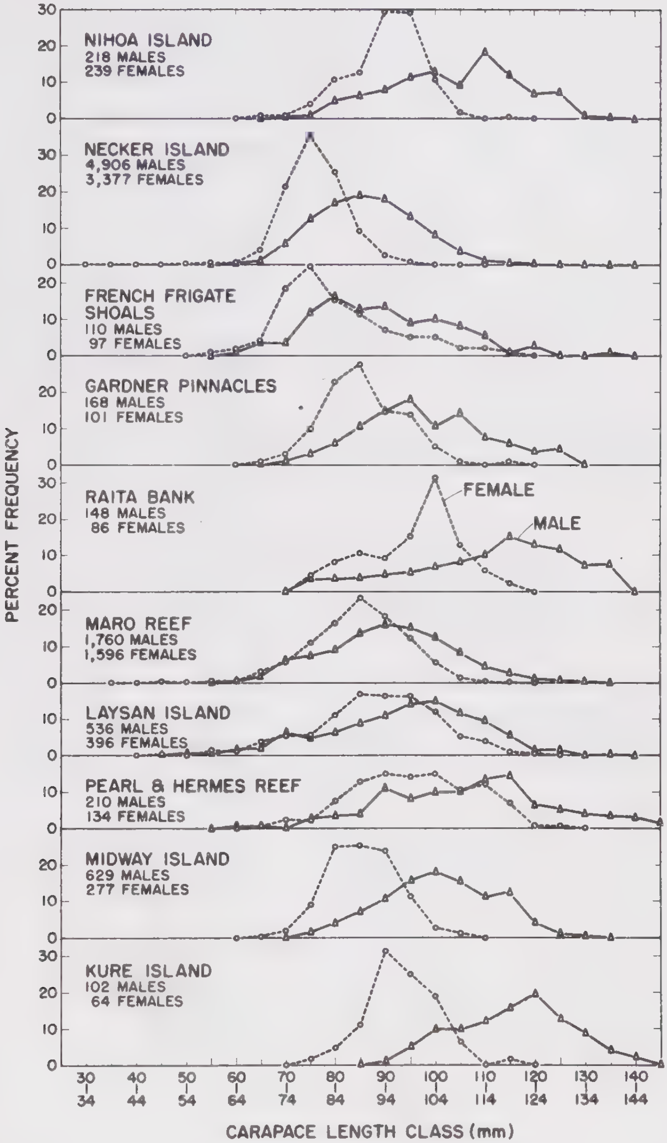

Figure 1. Percentage of frequency distributions of carapace lengths of male and female spiny lobsters sampled in waters of the Northwestern Hawaiian Islands, October 1976 to November 1978

TABLE 1. THE SIZE RANGE, MEAN CARAPACE LENGTH, STANDARD DEVIATION, AND VARIANCE OF MALE AND FEMALE SPINY LOBSTERS SAMPLED IN THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976-NOVEMBER 1978

	Male				Female			
Island or Bank	Size Range (mm)	Mean Carapace Length (mm)	Standard Deviation	Variance	Size Range (mm)	Mean Carapace Length (mm)	Standard Deviation	Variance
Nihoa	72-136	106.02	13.20	174.31	67-117	92.40	7.17	51.39
Necker	44-137	88.32	10.24	104.80	34-105	78.14	5.96	35.54
French Frigate Shoals	60-135	91.32	13.78	190.02	56-116	82.40	11.69	136.60
Gardner Pinnacles	72-128	99.96	12.49	155.96	68-117	87.61	8.00	64.08
Raita Bank	75-139	113.18	15.92	253.60	75-117	97.41	9.41	91.04
Maro Reef	47-133	92.97	12.71	161.47	44-119	86.67	9.77	95.54
Laysan	52-139	95.96	14.67	215.25	45-124	90.07	12.43	154.44
Pearl and Hermes	61-148	108.97	16.44	270.16	68-129	98.21	11.78	138.87
Midway	75-134	102.92	11.01	121.30	67-109	87.55	6.74	45.38
Kure	91-143	117.80	11.12	123.60	79-119	95.55	7.01	49.20

TABLE 2. THE SAMPLE SIZE, SIZE RANGE, MEAN CARAPACE LENGTH, STANDARD DEVIATION, AND VARIANCE OF MALE AND FEMALE SPINY LOBSTERS SAMPLED AT NECKER ISLAND, OCTOBER 1976-NOVEMBER 1978

	Male					Female				
Period	N	Size Range (mm)	Mean Carapace Length (mm)	Standard Deviation	Variance	N	Size Range (mm)	Mean Carapace Length (mm)	Standard Deviation	Variance
Oct.-Nov. 1976	690	48-118	87.03	10.47	109.62	233	59-97	77.22	5.70	32.44
May-June 1977	22	74-109	88.14	9.81	96.22	23	72-87	77.74	3.99	15.93
Sept.-Nov. 1977	466	49-137	91.08	12.86	165.47	372	50-105	80.94	8.19	67.14
Jan.-Mar. 1978	53	44-121	90.17	15.19	230.68	48	63-97	83.96	7.58	57.44
Oct.-Nov. 1978	268	52-111	86.97	9.70	94.13	183	34-93	77.70	8.06	64.96

reported that juvenile P. marginatus occur in inshore reef areas throughout the year. Furthermore, little is known about their behavior. One would expect, however, that at least greater numbers of lobsters smaller than the 45 to 49-mm length class would be caught in our fish traps, which are covered with 2.5-cm square wire mesh (as compared to the 5.1 x 10.2-cm mesh of our lobster pots). The low numbers of smaller size classes seen in the catch reflect either their scarcity on the trapping grounds or are simply not catchable; therefore, it can be expected that it is in the 45 to 49-mm size range that recruitment to the fishery is occurring.

There is no particularly striking trend in the average size of the lobsters geographically (Figure 1). The average size of the males was largest at Kure, at the northwestern tip of the NWHI chain followed by those caught at Raita Bank, which is located approximately halfway between Kure and Niihau. Among females, the average size was largest at Pearl and Hermes, followed by that at Raita Bank.

In all the areas sampled, the males were consistently larger than the females. The difference in average size between the sexes quite likely results from dimorphism related to egg bearing in females (Heydorn, 1969).

Proportion of legal-sized lobsters in the catch

In Hawaii, the regulation defines a legal-sized lobster as not less than 0.45 kg (1 lb) in weight or 8.25 cm in CL. During our surveys, we found a preponderance of legals in the overall lobster pot catches in the NWHI. Table 3 shows the breakdown of the legal and sublegal catches by sex, the male:female ratio among legals and sublegals, and the overall male:female and legal:sublegal ratios in 12 of the areas sampled. The ratios of legal:sublegal lobsters in the catch, by areas, varied widely between 53:47 at Necker and 99:1 at Kure Island with the overall arithmetic mean of the ratios reaching 85:15. The high proportion of legals in the catches, particularly at Raita Bank, Pearl and Hermes, Midway, and Kure can also be seen in Figure 1.

The percentage of sublegals caught by the lobster pots would tend to be relatively low, in part, due to various sampling artifacts. The mesh size used in the lobster pot construction usually permits most sublegals to escape or drop out during hauling. In addition, the effects of the molt cycle on the composition of the catches is unknown at present. McGinnis (1972) reported that juveniles of spiny lobsters molt more frequently than adults; therefore, newly molted juveniles would tend to remain secluded and, hence, not be subject to capture. Furthermore, the initial catch rates at any given locality would tend to include a large proportion of the large, older individuals, particularly males, because of their aggressive behavior.

Dominance hierarchy, which has been reported for the Australian lobsters (Chittleborough, 1974), exists in a natural environment for shelter and for food; however, in a fishery, the baited trap apparently becomes an object for which dominance behavior is displayed. This trait among large lobsters was quite evident in the changes in the proportion

TABLE 3. THE LEGAL TO SUBLEGAL AND MALE TO FEMALE RATIOS AMONG CATCHES MADE IN THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976-NOVEMBER 1978

	Legal			Male: Female Ratio	Sublegal			Male: Female Ratio	Total Male	Total Female[2]	Male: Female Ratio	Legal: Sublegal Ratio
	Male (No.)	Female[1] (No.)	Total (No.)		Male (No.)	Female[1] (No.)	Total (No.)					
Nihoa	104	81	185	56:44	5	8	13	38:62	109	146	43:57	93:7
Nihoa West Bank	86	46	132	65:35	3	3	6	50:50	89	72	55:45	96:4
Necker	2,909	465	3,374	86:14	1,175	1,841	3,016	39:61	4,084	2,963	58:42	53:47
French Frigate Shoals	51	24	75	68:32	20	31	51	39:61	71	55	56:44	60:40
Gardner Pinnacles	155	59	214	72:28	12	25	37	32:68	167	99	63:37	85:15
Raita Bank	106	60	166	64:36	2	1	3	67:33	108	61	64:36	98:2
Maro Reef	468	342	810	58:42	110	100	210	52:48	578	636	48:52	79:21
Laysan Island	295	193	488	60:40	33	32	65	51:49	328	247	57:43	88:12
Lisianski Island	2	5	7	29:71	2	0	2	100:0	4	5	44:56	78:22
Pearl and Hermes Reef	137	76	213	64:36	7	4	11	64:36	144	88	62:38	95:5
Midway Islands	370	110	480	77:23	14	28	42	33:67	384	152	72:28	92:8
Kure Island	97	53	150	65:35	0	2	2	0:100	97	60	62:38	99:1
Total	4,780	1,514	6,294	--	1,383	2,075	3,458	--	6,163	4,485	--	--
Arithmetic mean:				64:36				47:53			57:43	85:15

[1] Excludes berried females
[2] Includes berried females

of legals in the catches at Necker. For example, in November 1976 when trapping operations first began, the ratio of legal to sublegal reached 60:40 but dropped to 43:57 by May 1977 and was only 34:66 in August 1977 (Table 4). The drop in the proportion of legals is attributable to heavy fishing pressure exerted by the commercial fishing vessels resulting in removal of large dominant lobsters from the stock.

TABLE 4. CHANGES WITH TIME IN THE PROPORTION OF LEGAL-SIZED LOBSTERS IN THE CATCHES AT ONE 0.1° SQUARE NORTH OF NECKER ISLAND

Date	Legal (No.)	Sublegal (No.)	Ratio of legal to sublegal
November 1976	114	77	60:40
May 1977	157	212	43:57
August 1977	194	383	34:66

Sex ratio

Dominance behavior exists not only among large lobsters over smaller ones but also between sexes (Table 3). Among the areas sampled, only Lisianski shows the proportion of legal males below 50:50 in the catch; however, the ratio probably is not representative of the population at Lisianski because of the very small numbers of lobsters, both legals and sublegals, caught at that location. Excluding Lisianski, then, the sex ratios of the catches of legals from all areas varied from 86:14 at Necker to 56:44 at Nihoa. Among sublegals, and excluding areas with less than 10 lobsters sampled, we found a preponderence of females in five of the eight areas sampled with sex ratios of male:female varying between 64:36 to Pearl and Hermes and 32:68 at Gardner Pinnacles. The overall sex ratios, which include legals, sublegals, and berried females, varied from 72:28 at Midway to 43:57 at Nihoa (excluding Lisianski). The ratio of male:female in all the catches made in the NWHI was 57:43.

Reproductive cycle

The frequency of berried lobsters among the females in the population can be used as an index of the reproductive cycle. To delineate the breeding cycle among females in the different stocks in the NWHI, the percentages of berried females were calculated for months in which the catch was made and are shown in Figure 2. Unfortunately, the observations in most of the areas are inadequate to construct consecutive monthly distributions of berried females. Time, distance, and area to be covered prohibited more frequent visits to the survey areas; however, the data that are available give us some evidence of a trend in the time of high incidence of berried females in the catch and, hence, in the reproductive period.

The incidence of berried females in the catches at Nihoa, Necker, and French Frigate Shoals appears to be concentrated in the late summer and fall, and possibly into the winter months. Moving northwestward

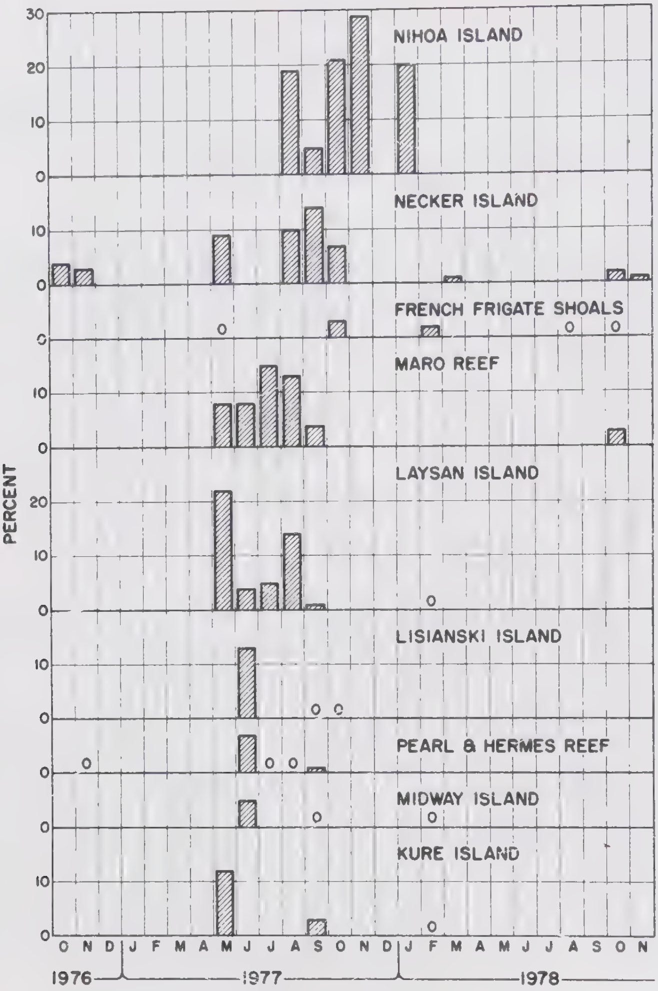

Figure 2. Percentage of berried females in the catches, by area, October 1976 to November 1978

along the chain, we found a gradual shift in the position of the monthly peaks to May and June. Comparison of our results with those obtained by MacDonald and Thompson (in preparation) at Midway shows good agreement with the peak numbers of berried females they found from May through August.

Relationship between carapace length and total weight

In the lobster fishery, both length and weight are used as criteria of harvest--the minimum legal size CL is used by the fishermen at sea, because this attribute can be measured more easily and accurately than weight, and weight is used as a criterion of harvest or total catch.

For the calculation of the relationship between CL and total weight, 605 measurements on lobsters caught at Necker, Maro Reef, and French Frigate Shoals during cruise TC-78-04 were used. For this preliminary report, data from all three areas were combined and calculations were made only for males and females, because it has been reported by Heydorn (1969) that growth is sexually dimorphic and that it may be related to egg bearing among females. All lobsters measured and weighed were intact with no appendages missing and none of the females was berried.

An exponential model, $W = aCL^b$, was fitted to the data for both male and female by the method of least squares. The 408 males ranged in size from 48.1 to 121.3 mm CL, whereas the 197 females ranged from 51.9 to 114.7 mm CL. The length-weight relationships for male and for female *P. marginatus* are as follows:

$$\text{Males:} \quad W = 0.00423\ CL^{2.6246}$$
$$\text{Females:} \quad W = 0.00090\ CL^{2.9952}$$

where W = weight in grams
CL = carapace length in millimeters
a and b = constants

The relationships are shown in Figure 3. For lobsters having a CL of 8.25 cm, the equations predict a total weight of 453.2 g (1 lb, 0 oz) for males and 496.0 g (1 lb, 1.5 oz) for females.

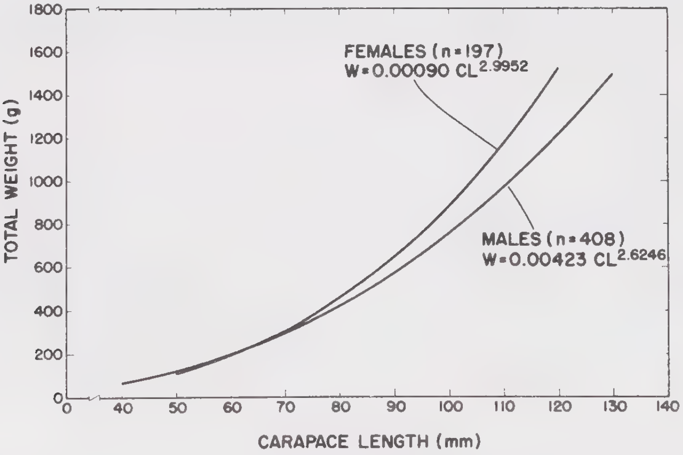

Figure 3. Length-weight relationship of male and female *Panulirus marginatus* determined from samples collected at Necker Island, French Frigate Shoals, and Maro Reef during cruise TC-78-04

It is interesting to note that males are slightly heavier than females at CL below 65 mm. At 65 mm CL, the males and females attain almost identical weights. From about 70 mm CL, the females are heavier, as compared with males of equivalent size and this difference can be attributed to an increase in tail weight in relation to total weight among females. Berry (1971) reported that elongation of the legs and enlargement of the cephalothorax among the South African lobster, P. homarus, accounted for the decrease in tail weight relative to total weight with increased size in males.

Relationship between carapace length and tail weight

Because accurate weighing of samples at sea is difficult due to the motion of the vessel, we believed it advisable to weigh the tails when fresh, frozen, and thawed to determine the variability when these attributes were regressed against CL. According to our preliminary analysis, frozen tail weight showed the least amount of variability about the line of best fit (i.e., had a higher correlation value). Furthermore, the differences in frozen and fresh weight, and frozen and thawed weight, were very small in almost all the samples collected. Therefore, in this report, frozen tail weight is used exclusively, because this attribute can be weighed rather precisely in the laboratory.

For enforcement purposes in situations where a vessel lands only frozen tails, it is useful to know the relationship between CL and frozen tail weight, provided that the former is used as a criterion for minimum legal size. During TC-78-04, 623 such measurements were collected. Carapace lengths of 402 males varied from 48.1 to 121.3 mm; for 221 females, CL varied between 51.9 and 114.7 mm.

An exponential model was fitted to the data for males and for females and the relationships are as follows:

$$\text{Males: } TW = 0.00731\ CL^{2.2536}$$
$$\text{Females: } TW = 0.00094\ CL^{2.7675}$$

where TW = tail weight in grams
CL = carapace length in millimeters

The equations predict that male lobsters with a CL of 8.25 cm would have a tail weight of 152.3 g (5.4 oz) and that female lobsters of minimum legal size would have a tail weight of 190.3 g (6.7 oz).

DISCUSSION AND CONCLUSIONS

The analysis by Uchida and co-workers indicated that the spiny lobster is distributed widely from Nihoa to Kure in the NWHI. Data on CL collected during our surveys showed striking differences in the average sizes of the unexploited population among the areas visited. Necker Island, for example, which had the highest catch rates, had the smallest average sizes among both males and females. Considering that the average sizes were small even at the outset of the survey, it is possible that there is a density dependent effect of stock size on growth rate caused by intraspecific competition. Such an effect could produce a larger population and may account for the high catch rates at Necker Island.

Because P. marginatus is endemic to the Hawaiian Archipelago and has been reported only from Johnston Atoll outside the Hawaiian chain, the resident population in the NWHI must be regarded as the source of larval recruits. Unfortunately, very little is known about the pelagic existence of the phyllosoma larvae of P. marginatus and the current patterns around the NWHI. It is possible that phyllosoma larvae emerging in waters of the Hawaiian Islands are carried out to sea by the prevailing surface currents only to be redeposited on substrates around the Hawaiian Archipelago. It is also possible that most of the phyllosoma larvae remain in coastal waters with little or no long-distance movement involved and that local repopulation is occurring. Whatever the mechanism, it is quite apparent that the distribution and abundance of the adults are dependent, to a large extent, on adaptation of the larvae to prevailing oceanographic conditions.

FUTURE RESEARCH NEEDS

To monitor changes in the population structure, we need to continue sampling at banks where relatively little fishing effort has been expended in order to expand our data base on distribution, apparent abundance, CL, weight, and other morphometric characteristics. There is also a need to continue collection of data on berried females to delineate the reproductive cycle.

To study the occurrence of the puerulus, we have built Withan larval collectors, which will be placed at selected sites, and we will also expand our night-light observational program. Traps with enlarged openings are presently being used in attempts to capture individuals larger than 14 cm CL, which have been taken in our traps only infrequently.

SUMMARY

The present study elucidated several aspects of the unexploited populations of P. marginatus in the NWHI and some of the results appear to be particularly significant. Analysis of our data showed that there were striking differences in the average sizes of lobsters among the various islands and banks surveyed. The stock at Necker Island, in particular, presented an interesting contrast to that found elsewhere in the NWHI chain. At Necker, our surveys revealed that the average size of both males and females was the smallest and this phenomenon was evident even during our first survey at this island.

Our initial surveys also revealed that the proportion of legal-sized lobsters was relatively high in most areas and that males predominated in the catch. Data on egg-bearing females in the catch disclosed that there is a marked seasonality in reproduction with peaks in early summer to fall.

The length-weight relationships predicted that an 8.25 cm CL lobster would weigh 453.2 g for males and 496.0 g for females. This differential growth between the sexes was attributed to an increase in tail weight in relation to total weight among females as a result of egg bearing. The relationship between CL and tail weight predicted that legal-sized males would have a tail weight of 152.3 g as opposed to 190.3 g in females.

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BIOLOGY, DISTRIBUTION, AND ESTIMATES OF APPARENT ABUNDANCE OF THE SPINY LOBSTER, *PANULIRUS MARGINATUS* (QUOY AND GAIMARD), IN WATERS OF THE NORTHWESTERN HAWAIIAN ISLANDS:

PART I. DISTRIBUTION IN RELATION TO DEPTH AND GEOGRAPHICAL AREAS AND ESTIMATES OF APPARENT ABUNDANCE

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ABSTRACT

This paper describes the results of field surveys conducted by the Honolulu Laboratory on the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Of 17 islands and submerged banks surveyed from October 1976 to November 1978, only Necker Island and Maro Reef had sufficiently large stocks of spiny lobsters to warrant commercial exploitation. The distribution of spiny lobsters in relation to geographical area and depth is also discussed. Future research needs are identified, including specialized data on the environment and the stocks to estimate their magnitude and potential yield, data on seasonal and spatial variation in stock distribution and abundance, and observations on behavior of spiny lobster in relation to biological and environmental conditions.

Northwestern Hawaiian Islands
spiny lobster
distribution
apparent abundance

INTRODUCTION

The Northwestern Hawaiian Islands (NWHI), often called the "Leeward Islands," are part of the Hawaiian Archipelago comprising a chain of small islands, islets, rocks, and shoals stretching 1,250 nmi west northwest of Niihau (Figure 1). All the land areas except Midway, which is a state-administered wildlife sanctuary and the site of a Coast Guard loran station, constitute the Hawaiian Islands National Wildlife Refuge and are seldom visited.

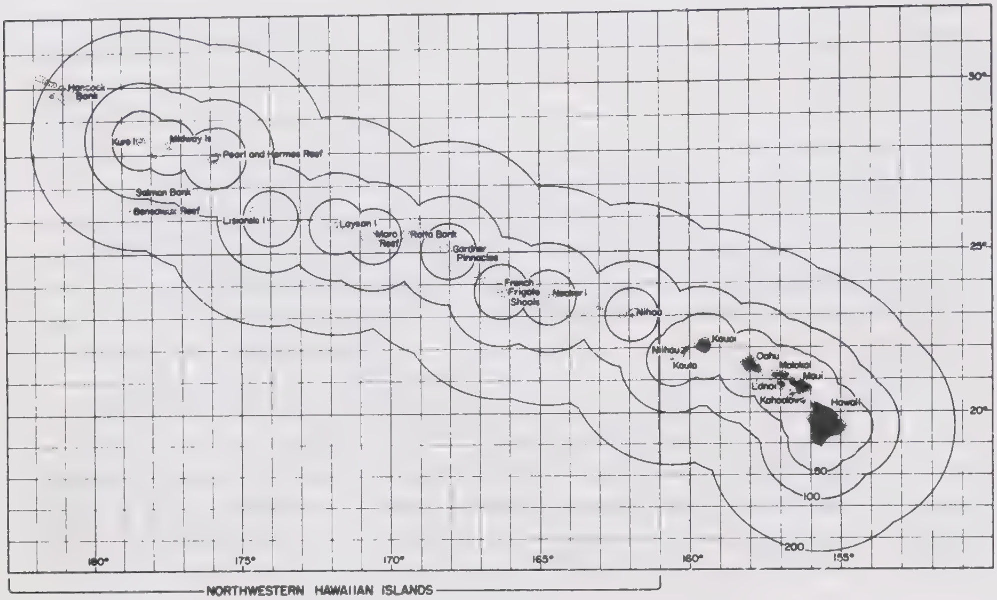
Hancock Bank
Kure I.
Midway Is
Pearl and Hermes Reef
Salmon Bank
Bensdoux Reef
Lisianski I.
Laysan I.
Maro Reef
Raita Bank
Gardner Pinnacles
French Frigate Shoals
Necker I.
Nihoa
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Kahoolawe
Hawaii
50
100
200
30°
25°
20°
180°
175°
170°
165°
160°
155°
NORTHWESTERN HAWAIIAN ISLANDS

Figure 1. The Hawaiian Archipelago

In 1969, the Governor's Task Force on Oceanography of the State of Hawaii, recognizing the increase in fishing pressure being exerted on the fishery resources of Hawaii's main islands, recommended exploration and possible development of the fishery resources in waters of the NWHI (State of Hawaii, 1969, 1974). In response to these recommendations the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), reconnoitered waters of the NWHI on a cruise of the NOAA ship David Starr Jordan in 1973 and followed that with two research cruises on the NOAA ship Townsend Cromwell in 1975.

In 1976, NMFS launched a full-scale investigation of the NWHI. Realizing that the extent of the investigation was beyond the capabilities of the staff and facilities of any single research agency in Hawaii, NMFS proposed a cooperative research effort with the Hawaii Division of Fish and Game (HDFG) and the U.S. Department of the Interior, Fish and Wildlife Service (USFWS). From the proposal evolved the Tripartite Cooperative Agreement which, in effect, gave responsibility for survey and assessment of the inshore fishery resources to the HDFG and for land-associated resources such as sea and land birds to the USFWS. The Honolulu Laboratory assumed responsibility for developing a quantitative fishery survey and assessment of the slope and coastal pelagic fish resources. A short time after the formation of the tripartite agreement, a fourth agency, the University of Hawaii Sea Grant College Program, became an active participant in the investigation.

Initially, very little was known about the slope and coastal pelagic resources in the NWHI; therefore, our objectives during the first two years of the investigation were simply to conduct exploratory fishing to determine the kinds of fish, shellfish, and molluscs present in waters of the NWHI, their spatial and temporal distribution, and their relative abundance in waters of the several islands and submerged banks. In this report, we summarize trapping results for the spiny lobster, *Panulirus marginatus*, from October 1976 to November 1978 aboard the *Townsend Cromwell* and a commercial fishing vessel chartered for two trips.

At the outset of our survey, we identified nearly 50 islands, submerged banks, and seamounts within 200 nmi of the NWHI. We have surveyed 17 of these for spiny lobster and this report covers what we found in waters around these islands and banks.

METHODS

Data used in this report were collected on six survey cruises of the *Cromwell* (TC-76-06, TC-77-02, TC-77-03, TC-78-01, TC-78-03, and TC-78-04) and on two NMFS-chartered cruises of the commercial fishing vessel *Easy Rider* (ER 77-02, Parts I and II) which operates out of Honolulu.

The standard gear used on all our lobster trapping operations was the California two-chambered lobster pot. In conjunction with our surveys of bottom fish resources, the large, Hawaiian-type fish trap was also used at the lobster trapping stations. Both the lobster pot and fish trap have been described in detail by Uchida and Hida (1977).

The fish traps were effective not only in capturing a wide variety of fish but also, as incidental catches, spiny lobsters. This report, however, covers only the data collected at our lobster trapping stations. Data on lobster catches made by the fish traps were used only to supplement that obtained on certain highly productive areas, to determine recruitment of juveniles, and for studies involving the length-frequency distributions of the stock(s).

To determine distribution and estimate relative abundance of spiny lobsters, banks were divided into a network of equal area squares or sampling units, measuring 0.1° to a side of latitude and longitude. Each square was identified by a six-digit code at the lower right corner. The first two digits give the whole latitude, the third identifies the 0.1° of latitude which is numbered from 0 to 9 starting at 00' of latitude. The fourth and fifth digits give the whole longitude minus 100, and the last digit identifies the 0.1° of longitude from 0 to 9 starting at 00' of longitude. For example, 220615 identified the square located at lat. 22°00'N and long. 161°30'W. When catches fell on a latitudinal line bordering a square, they were assigned to the square directly above; when they fell on a longitudinal line of a square, they were assigned to the square directly to the left (Figure 2).

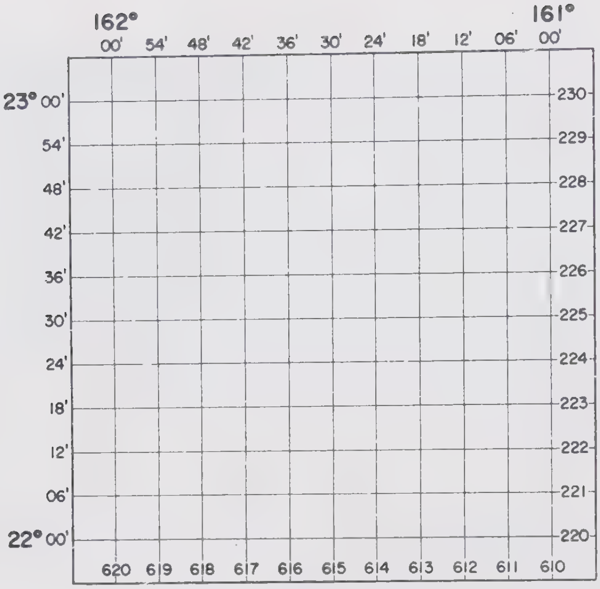
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Figure 2. Codes for 0.1° squares established for the Northwestern Hawaiian Islands

RESULTS

Species composition

Our lobster trapping stations produced a great diversity of arthropods, molluscs, and fishes. Although Morris (1968) indicated that two species of spiny lobsters--*P. marginatus* and *P. penicillatus*--are commonly caught in waters around the major islands, our trapping stations produced none of the latter, primarily because it is essentially a shallow-water species that inhabits waters usually less than 5.5 m (3 fathoms) deep (De Bruin, 1962).

The second most important species caught in the lobster pots was the slipper lobster, *Scyllarides squammosus*.[1] Other commercially valuable species included the frog crab, *Ranina ranina*, octopus, *Polypus marmoratus*, pink snapper, *Pristipomoides filamentosus*, sea bass, *Epinephelus quernus*, amberjack, *Seriola dumerili*, and the thick-lip carangid, *Caranx cheilio*.

Distribution of fishing effort and apparent abundance

Confining our analysis to data collected with lobster pots during our survey and charter cruises between October 1976 and November 1978, 4,835 trap-nights were fished in waters of the NWHI producing 13,214 spiny lobsters for an overall catch rate of 2.73 lobsters/trap-night (Table 1). Catch rates varied considerably among the areas visited, ranging from 0.00 at Middle Bank, Pioneer Bank, and at No-name Bank #8 to 4.72 lobsters/trap-night at Necker Island.

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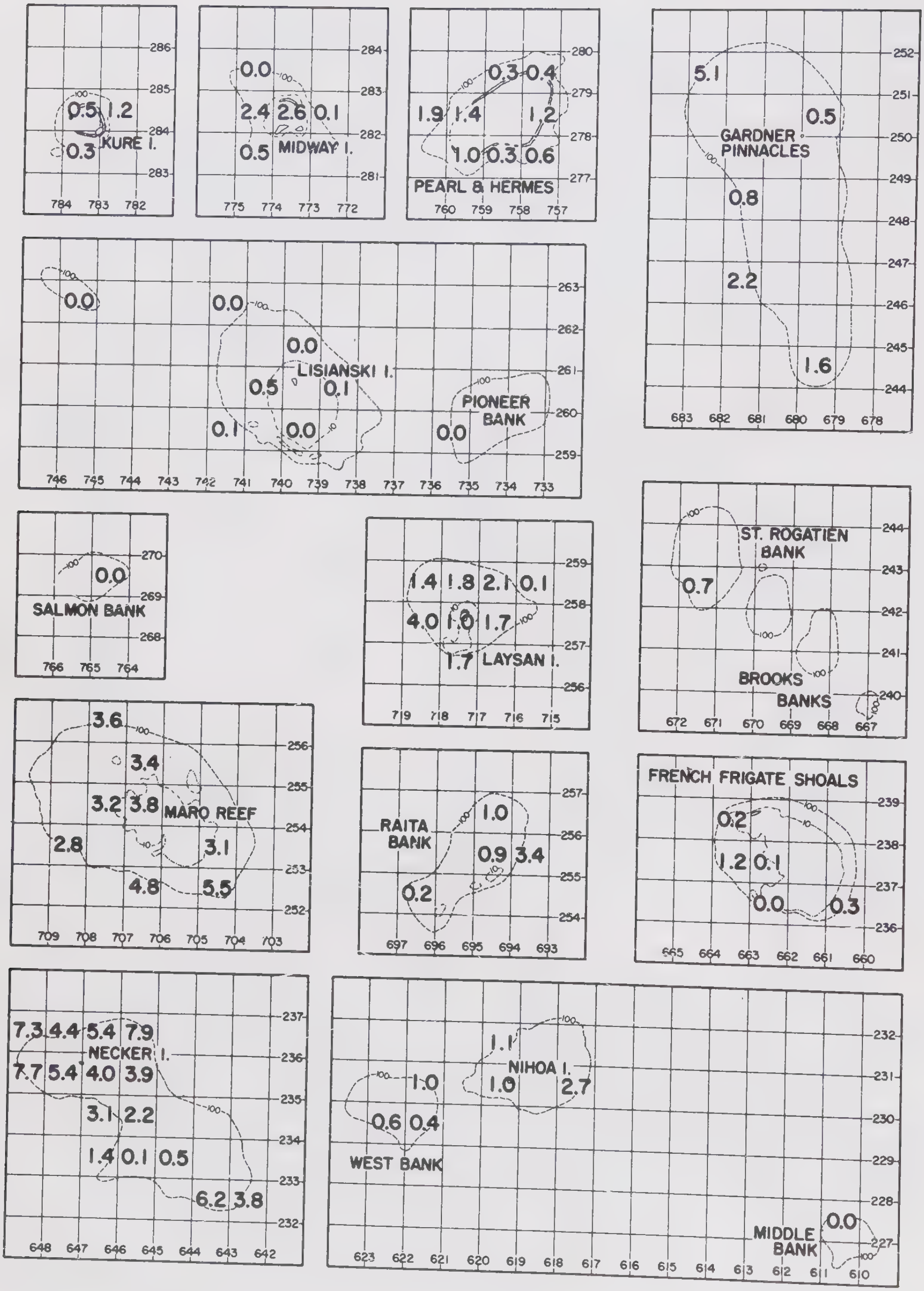
[1] We were informed recently by Dr. Craig MacDonald, University of Hawaii, Department of Zoology, Honolulu, Hawaii that in addition to *S. squammosus*, a second species, *S. haanii*, may be present in Hawaiian waters.

TABLE 1. THE POSITION OF THE ISLANDS, BANKS, AND REEFS, TOTAL NUMBER OF LOBSTERS CAUGHT, NUMBER OF TRAP-NIGHTS OF EFFORT EXPENDED, AND CATCH/TRAP-NIGHT OF ALL LOBSTERS INCLUDING LEGALS (8.25 CM OR MORE IN CARAPACE LENGTH), SUBLEGALS, AND BERRIED FEMALES IN THE NORTHWESTERN HAWAIIAN ISLANDS. CATCH DATA ARE FOR OCTOBER 1976-NOVEMBER 1978

Island or Bank	Position		Total Catch (No.)		
	Latitude (N)	Longitude (W)	Catch	Trap-Night	Catch/ Trap-Night
Middle Bank	22°42'	161°02'	0	40	0.00
Nihoa	23°03'	161°55'	255	178	1.43
Nihoa (west bank)	22°58'	162°14'	161	218	0.74
Necker Island	23°34'	164°42'	7,937	1,680	4.72
French Frigate Shoals	23°46'	166°18'	140	359	0.39
St. Rogatien Bank	24°25'	167°15'	41	59	0.69
Gardner Pinnacles	25°01'	167°59'	307	209	1.47
Raita Bank	25°35'	169°35'	169	92	1.84
Maro Reef	25°29'	170°35'	2,684	663	4.04
Laysan Island	25°42'	171°44'	575	341	1.69
Pioneer Bank	26°00'	173°25'	0	24	0.00
Lisianski Island	26°02'	174°00'	9	179	0.05
No-name Bank #8	26°17'	174°34'	0	24	0.00
Salmon Bank	26°56'	176°28'	2	48	0.04
Pearl and Hermes Reef	27°48'	175°51'	232	236	0.98
Midway Islands	28°12'	177°22'	576	280	2.06
Kure Atoll	28°25'	178°25'	158	240	0.66
Total			13,214	4,835	2.73

It is quite evident that spiny lobsters are distributed throughout the entire NWHI chain from Nihoa to Kure (Table 1 and Figure 3). The data also show that the shelves surrounding Necker and Maro Reef were the most productive during the survey period. Necker, because of its proximity to Oahu where the lobster fleet is based, received considerable trapping effort from the commercial boats only months after the Cromwell obtained catch rates as high as 17.80 lobsters/trap-night in some areas around the island during the October-November 1976 cruise. During our surveys, we expended 1,680 trap-nights at Necker and caught 7,937 lobsters or an average of 4.72 lobsters/trap-night.

Maro Reef, which was found to be almost as productive as Necker, was first visited and fished with significant amounts of effort during cruise TC-77-02 (Part III) in May-June 1977. In the course of our


KURE I.
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286 285 284 283
784 783 782
MIDWAY I.
0.0
2.4 2.6 0.1
0.5
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775 774 773 772
PEARL & HERMES
0.3 0.4
1.9 1.4 1.2
1.0 0.3 0.6
280 279 278 277
760 759 758 757
GARDNER PINNACLES
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0.5
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252 251 250 249 248 247 246 245 244
683 682 681 680 679 678
LISIANSKI I.
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0.5 0.1
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PIONEER BANK
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263 262 261 260 259
746 745 744 743 742 741 740 739 738 737 736 735 734 733
SALMON BANK
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270 269 268
766 765 764
LAYSAN I.
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4.0 1.0 1.7
1.7
259 258 257 256
719 718 717 716 715
ST. ROGATIEN BANK
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BROOKS BANKS
244 243 242 241 240
672 671 670 669 668 667
MARO REEF
3.6
3.4
3.2 3.8
2.8 3.1
4.8 5.5
256 255 254 253 252
709 708 707 706 705 704 703
RAITA BANK
1.0
0.9 3.4
0.2
257 256 255 254
697 696 695 694 693
FRENCH FRIGATE SHOALS
0.2
1.2 0.1
0.0 0.3
239 238 237 236
665 664 663 662 661 660
NECKER I.
7.3 4.4 5.4 7.9
7.7 5.4 4.0 3.9
3.1 2.2
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6.2 3.8
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648 647 646 645 644 643 642
NIHOA I.
1.1
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WEST BANK
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MIDDLE BANK
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623 622 621 620 619 618 617 616 615 614 613 612 611 610
100

Figure 3. Distribution of spiny lobster catch rates, by 0.1° squares in the Northwestern Hawaiian Islands, October 1976-November 1978

surveys, we expended 663 trap-nights and caught 2,684 lobsters or an average of 4.04 lobsters/trap-night (Table 1).

Gardner Pinnacles, Raita Bank, and Laysan were other islands and banks that showed some highly productive areas; however, the overall catch rates never approached the magnitude we found for Necker and Maro Reef. These areas all require additional surveys to determine their productivity.

Relation between catch per trap-night and depth

Panulirus marginatus has been reported to occur at depths ranging from a few meters to 183 m in the Hawaiian Islands (McGinnis, 1972). To examine the relative abundance of this species with respect to depth in the NWHI, we grouped the catch data into 9-m (5-fathom) strata for each of the islands and banks. The relative abundance of *P. marginatus* at the lower end of the NWHI chain was higher at depths between 37 and 64 m (21 and 35 fathoms); however, in the middle and higher latitudes particularly from Gardner Pinnacles to Kure, there was a tendency for the catch/trap-night to be higher usually in waters 10 to 36 m (6 to 20 fathoms), except at Midway where the relative abundance of spiny lobsters was highest at 37 to 45 m (21 to 25 fathoms) (Figure 4). The relatively low catch rates we observed in waters deeper than 64 m (35 fathoms) in the northern part of the chain may be the consequence of differences in temperature regime from north to south.

Data from XBT casts made during two cruises of the *Cromwell* were examined for differences in the surface and subsurface (0-140 m) temperature at Necker and Midway (Table 2). It is evident that during both summer and winter, there is a pronounced cooling of the subsurface waters around Midway. Also of interest is the depth of the mixed layer, which is relatively shallow in summer and deep in winter. These data are similar to the results obtained by Seckel (1962) who studied the oceanographic climate of the Hawaiian Islands region.

DISCUSSION AND CONCLUSIONS

The pattern that emerges from our trapping results in the NWHI is one of uneven distribution of spiny lobsters with heavy concentrations located only at Necker and Maro Reef. There are, however, other sites such as Gardner Pinnacles, Raita Bank, and Laysan that show potential, but only additional surveys or commercial fishing at these locations will provide sufficient data to verify the potential. Furthermore, because fishing is still in its infancy, it is extremely difficult to draw inferences about catch rates. Catch/trap-night for spiny lobsters is influenced by dominance behavior of the large adults, of adult males, and perhaps by reproductive condition of the females.

Another interesting aspect of the distributional pattern of *P. marginatus* is its relationship to depth and possibly subsurface temperatures prevailing over the substrate. Whereas the catch/trap-night was relatively high in depths between 37 and 64 m around islands and banks southeast of Gardner Pinnacles, there was a trend for catch/trap-night

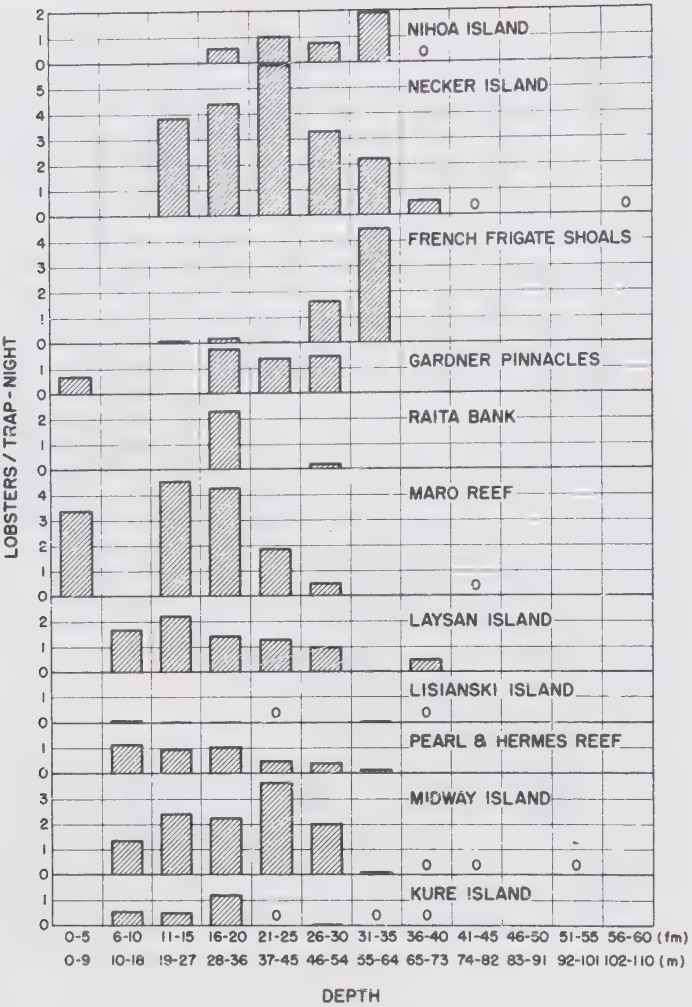

Figure 4. Distribution of spiny lobster catch rates, by depth, in the Northwestern Hawaiian Islands, October 1976-November 1978

to be higher at shallower depths between Gardner Pinnacles and Kure. In addition to the possible effects of subsurface temperatures on the depth distribution pattern of spiny lobsters, other factors such as substrate type and location of feeding or browsing pastures may also influence habitat selection.

At this time, nothing is known about the pattern of larval recruitment in the NWHI. Johnson (1968) reported catching spiny lobster phyllosoma in plankton samples at a number of locations in the Hawaiian Archipelago. Whereas the phyllosoma of both P. marginatus and P. penicillatus was collected around Oahu and in waters to the southwest

TABLE 2. SURFACE AND SUBSURFACE TEMPERATURES IN WATERS AROUND NECKER AND MIDWAY ISLANDS DURING THE SUMMER AND FALL MONTHS IN 1976-77

Depth (m)	Summer Temperature °C Necker (May 17, 1977)	Summer Temperature °C Midway (May 30, 1977)	Winter Temperature °C Necker (Oct. 17, 1976)	Winter Temperature °C Midway (Nov. 2, 1976)
0	24.9	24.9	25.8	26.1
10	24.7	24.4	25.7	26.1
20	24.4	23.9	25.7	26.1
40	24.2	22.8	25.7	26.1
60	23.9	21.2	25.7	26.1
80	23.1	20.4	25.3	23.6
100	22.2	19.6	23.1	21.6
120	21.9	19.2	22.0	21.3
140	21.7	18.7	21.0	18.5

of the main islands, Johnson found only P. marginatus phyllosoma at French Frigate Shoals. Thus, the distribution of these phyllosoma corresponds to some extent to the distributional pattern of the adults.

FUTURE RESEARCH NEEDS

Exploratory fishing to determine species composition and initial catch rates has been completed for most of the larger islands and banks in the NWHI. Several areas for future research include a need for specialized information on the environment and the stocks to estimate their magnitude and potential yield. Catch and effort data from commercial vessels are needed to calculate more precise catch rates. Additional studies are needed to determine how catch rates can be expected to change with increasing fishing pressure. We need a sufficiently large data base to be able to predict seasonal and spatial variation in stock distribution and year-to-year fluctuation in stock abundance or availability.

More research is also needed on the relationship between lobster behavior and changes in biological and environmental parameters, on predation of lobsters by large predators such as sharks and carangids, on gear competition, on ghost fishing, and on escape gaps.

The results of all these studies will assist us in making crucial decisions on the management of the fishery and will influence decisions of investors.

SUMMARY

The results of exploratory surveys conducted by the NMFS show that the spiny lobster, P. marginatus, is unevenly distributed throughout the NWHI. Two locations--Necker and Maro Reef--showed the highest concentrations; Gardner Pinnacles, Raita Bank, and Laysan showed signs of having good potential.

The study also revealed that the concentrations of lobsters are stratified by depth. South of Gardner Pinnacles, the highest catch rate occurred within 37 and 64 m, but around islands and banks to the north, the highest catch rate occurred between 10 and 36 m.

The exploratory phase of the NWHI investigation is well toward completion and future research needs are being considered.

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SURVEY OF THE PELAGIC FISHES OF THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Longline fishery catch statistics were used to estimate relative abundance of true pelagic species within the Fishery Conservation Zone of the Northwestern Hawaiian Islands. Relative apparent abundance of coastal pelagic species was determined by trolling surveys. Growth curves for *Euthynnus affinis* and *Thunnus alalunga* were estimated from otolith age determinations. A study of the fecundity of *Acanthocybium solandri* has begun.

fecundity
relative apparent abundance
Northwestern Hawaiian Islands
age and growth
pelagic fishes

INTRODUCTION

The survey area in the Northwestern Hawaiian Islands (NWHI) included in this study extends from Nihoa to Kure Atoll and is about 1,700 km long and 640 km wide. Much of this area is in the pelagic realm. The pelagic resources considered in this report consist of the true pelagic and the coastal pelagic fishes.

The foreign longline fishery in the Pacific has been harvesting the true pelagic fishes from an area northwest of the inhabited high islands. This fishing ground extends into the U.S. 200-mile Fishery Conservation Zone (FCZ) around the NWHI. The true pelagic species include the bigeye tuna, *Thunnus obesus*; yellowfin tuna, *T. albacares*; albacore, *T. alalunga*; northern bluefin tuna, *T. thynnus*; skipjack tuna, *Katsuwonus pelamis*; swordfish, *Xiphias gladius*; striped marlin, *Tetrapturus audax*; shortbill spearfish, *T. angustirostris*; blue marlin, *Makaira nigricans*; black marlin, *M. indica*; sailfish, *Istiophorus platypterus*; mahimahi, *Coryphaena hippurus*; and sharks, *Carcharhinus maou* (*C. longimanus*), *C. falciformis*, Isurus oxyrinchus, and Prionace glauca. Yong and Wetherall (1980) have estimated the foreign longline monthly effort and catch within the 200-mile FCZ for 1965 through 1977.

The Japanese baitboat fishery has also harvested skipjack, bigeye, and yellowfin tunas in the FCZ. In 1972, the eastward expansion of the albacore baitboat fishery reached the NWHI (Fisheries Agency of Japan, 1977a). Albacore was caught only in 1972, 1975, and 1977 in the vicinity of Hancock Seamounts. Yellowfin and bigeye tunas were caught primarily on or near the banks of the NWHI; skipjack tuna was also caught on or near the banks but was also caught in abundance on the open sea southwest of the FCZ (Fisheries Agency of Japan, 1977b; Yong and Wetherall, 1980). Catches of skipjack tuna, the target species, peaked for about a period of a month between May and August. Whereas the catch rates of skipjack tuna have averaged between 6 and 11 metric tons (MT)/vessel/day, single-day catches up to 50 MT a day have been reported (Tanaka, n.d.). Yong and Wetherall (1980) also estimated the monthly fishing effort and skipjack tuna catch within the 200-mile FCZ for 1972 through 1977.

Besides skipjack and yellowfin tunas, which are also considered as true pelagic species, the coastal pelagic species include the ono, Acanthocybium solandri; kawakawa, Euthynnus affinis; rainbow runner, Elagatis bipinnulatus; bigeye scad, Trachurops crumenophthalmus; Japanese mackerel, Scomber japonicus; and four species of mackerel scad, Decapterus macarellus (= D. pinnulatus), D. maruadsi, D. muroadsi (= D. russellii), and D. macrosoma. At present, a commercial fishery for the coastal pelagic resources does not exist in the NWHI. On a few occasions, lobster fishing vessels have trolled for kawakawa and yellowfin tuna to use as bait in lobster traps. Mahimahi and ono caught on trolling lines by lobster fishermen are sold at the Honolulu fish auction.

Research cruises to the NWHI were made on 30 occasions during the 1950s and 1960s and data on trolling and fish school and bird flock sightings from these cruises have been published by Murphy and Ikehara (1955), Graham (1957), and Waldron (1964). And prior to the current series of NWHI survey cruises, the NOAA ship Townsend Cromwell made a search-survey cruise for skipjack tuna in 1975 which included parts of the NWHI.

Except for these fish school surveys and some baitfish surveys in the NWHI, the pelagic resources have not been studied. Records of the foreign longline fishery and baitboat fishery provide us with estimates of relative apparent abundance of tunas and billfishes. This study includes the distribution, catch rates, age and growth, fecundity and spawning, and foraging habits of the coastal pelagic species.

MATERIAL AND METHODS

Trolling and tagging operations

The seven survey cruises of the Townsend Cromwell since the summer of 1977 included a standard trolling procedure. Nine lines were trolled at 7 knots during various times of the day at the edge of banks between the

73 and 274-m depth contours. When a fish was landed, it was measured for fork length, sexed, and sometimes weighed. Time of landing, position, and depth were also recorded on the Standardized Surface Trolling Data Sheet (SSTDS). Ovaries and stomach contents were preserved in a solution of 4% formaldehyde and seawater. Otoliths were extracted and frozen in water for examination at the laboratory.

Kawakawa, yellowfin tuna, and ono were tagged in 1977. Troll-caught fishes were measured, tagged with a dart tag (Yamashita and Waldron, 1958), and released.

Distribution and relative apparent abundance

Yong and Wetherall (1980) tabulated the catch and effort by 1° squares from Japanese and unpublished Taiwan longline fishery data for 1971 through 1975 and from Japanese baitboat data for 1972 through 1977. Catch and effort data were estimated by 5° squares for 1965 through 1970, 1976, and 1977. They estimated the catch of major tuna and billfish species and effort within the FCZ around the NWHI using these tabulations.

The distribution of troll-caught pelagic fishes was analyzed by comparing the number of fishes caught per line-hour of fishing in each 6-min cell around the NWHI. The position of capture on the SSTDS was used to place the fish into cells. When the position of capture was missing, the position was estimated using the ship's track chart and the time of capture.

Age and growth studies

In the laboratory, sagittae, the largest of the otoliths, were cleaned, etched, mounted, and read as described by Uchiyama and Struhsaker (in press). Age-length determinations were used to calculate the von Bertalanffy growth parameters.

Experiments were also conducted to verify that growth rings were deposited daily. At the Kewalo Research Facility, pelagic fishes maintained in aquaria were either injected or orally fed oxytetracycline at a rate of about 33 mg oxytetracycline/kg of fish to mark a spot on the sagittae. The daily deposition of growth rings was verified by matching the number of daily growth rings counted between the mark, which was visible under ultraviolet excitation, and the edge of the rostrum or postrostrum with the number of days the fish was kept alive and feeding after marking.

Fecundity and spawning season

Since 1978, all developing and ripe ovaries of pelagic fishes were collected to determine the length of the spawning period. Immature ovaries were noted in the remarks column of the SSTDS. The maturity of the ovary was determined on the basis of the most advanced ova present as described by Uchiyama and Shomura (1974). Then the monthly percentage distribution of sampled ovaries in each developmental stage, i.e., immature, developing, advanced developing, early ripe, and ripe, was calculated.

Fecundity estimates were made only on ovaries in the advanced developing, early ripe, and ripe stages. The ova development within an ovary was tested for homogeneity and fecundity estimates were made as described by Otsu and Uchida (1959).

Study on foraging habits

The volume and individual counts of forage items were determined for each stomach. Each item was identified to species when possible and measured for volume and length.

Night-light stations

A 1,500-W bulb night light was used to attract bigeye scad, mackerel scad, and other organisms. Dip nets and jig lines were used to capture organisms attracted to the light. Hourly data on organisms caught and estimates of the quantity of organisms attracted to the light were kept.

RESULTS

Distribution and relative apparent abundance

Annual catch rates of tunas and billfishes were estimated using catch and effort data obtained from foreign longline vessels operating within the FCZ around the NWHI (Table 1). The catch rate of the whole mixed species fishery remained stable during the 5 years of study, but fluctuations in the catch rates of individual species such as bigeye tuna, albacore, and striped marlin occurred. Although the longline fishery was a winter fishery in the 1970s (Figure 1), there was also a summer fishery in the 1960s. The estimated annual catch of major tuna species was obtained by combining the catch by longliners with the catch by the baitboats (Table 2).

Kawakawa was the species most frequently caught by trolling gear (Figure 2). Areas where large numbers of kawakawa were caught have remained productive for this species throughout the survey period. Yellowfin tuna was plentiful at Pearl and Hermes Reef. Trolling at Kure was very poor.

Trolling catch rates for coastal pelagic fishes decreased toward the northwest end of the chain (Table 3). This decrease could be due to environmental conditions, or to the pole-and-line fishing by the Japanese, or other factors. The catch rates of coastal pelagic fishes appeared to decline with time (Figure 3). A regression of catch rate on time produced a significant negative slope for both Nihoa ($P = 0.024$) and Laysan ($P = 0.006$) indicating a decline in apparent abundance over time.

TABLE 1. ESTIMATED ANNUAL CATCH, EFFORT, AND CATCH PER UNIT EFFORT BY FOREIGN LONGLINERS WITHIN 200 MILES OF THE NORTHWESTERN HAWAIIAN ISLANDS, 1971-75 (Yong and Wetherall, 1980)

Year	Species[1]	Effort		Catch		CPUE
		Days	Hooks	(kg)	(No.)	No./1,000 Hooks
1971	YF	1,592	3,184,000	467,437	9,872	3.10
	BE	—	—	820,988	19,155	6.02
	AL	—	—	397,875	15,658	4.92
	BF	—	—	1,121	6	0.00
	SJ	—	—	1,604	353	0.11
	All tunas	—	—	1,689,025	45,044	14.15
	BLM	—	—	81,496	838	0.26
	BM	—	—	2,700	56	0.02
	SM	—	—	261,192	8,583	2.70
	SWF	—	—	58,233	747	0.23
	SBSF, SF	—	—	8,271	512	0.16
	All billfishes	—	—	411,894	10,736	3.37
1972	YF	1,747	3,494,000	260,452	5,391	1.54
	BE	—	—	1,284,487	28,250	8.08
	AL	—	—	478,494	18,713	5.36
	BF	—	—	1,534	8	0.00
	SJ	—	—	1,982	273	0.08
	All tunas	—	—	2,026,949	52,635	15.06
	BLM	—	—	53,382	690	0.20
	BM	—	—	2,281	38	0.01
	SM	—	—	172,714	5,394	1.54
	SWF	—	—	178,456	2,289	0.66
	SBSF, SF	—	—	8,195	477	0.14
	All billfishes	—	—	415,028	8,888	2.54
1973	YF	985	1,970,000	132,825	2,706	1.37
	BE	—	—	496,445	10,244	5.20
	AL	—	—	348,159	15,150	7.69
	BF	—	—	1,661	8	0.00
	SJ	—	—	625	102	0.05
	All tunas	—	—	979,716	28,210	14.32
	BLM	—	—	17,695	251	0.13
	BM	—	—	1,087	14	0.01
	SM	—	—	78,215	2,966	1.50
	SWF	—	—	82,431	1,057	0.54
	SMSF, SF	—	—	9,951	559	0.28
	All billfishes	—	—	189,379	4,847	2.46
1974	YF	444	888,000	118,991	2,411	2.72
	BE	—	—	95,463	2,457	2.77
	AL	—	—	280,710	11,755	13.24
	BF	—	—	1,631	8	0.01
	SJ	—	—	547	108	0.12
	All tunas	—	—	497,345	16,739	18.85
	BLM	—	—	24,429	371	0.42
	BM	—	—	1,172	18	0.02
	SM	—	—	20,191	725	0.82
	SWF	—	—	41,981	538	0.61
	SBSF, SF	—	—	7,014	439	0.49
	All billfishes	—	—	94,787	2,091	2.35
1975	YF	832	1,664,000	170,677	3,798	2.28
	BE	—	—	512,260	11,792	7.09
	AL	—	—	169,695	7,446	4.47
	BF	—	—	1,652	8	0.00
	SJ	—	—	695	169	0.10
	All tunas	—	—	854,979	23,213	13.95
	BLM	—	—	13,766	178	0.11
	BM	—	—	649	11	0.01
	SM	—	—	69,622	2,447	1.47
	SWF	—	—	24,798	318	0.19
	SBSF, SF	—	—	6,775	408	0.24
	All billfishes	—	—	115,610	3,362	2.02

[1] YF = yellowfin tuna, *Thunnus albacares*; BE = bigeye tuna, *T. obesus*; AL = albacore, *T. obesus*; AL = albacore, *T. alalunga*; BF = bluefin tuna, *T. orientalis*; SJ = skipjack tuna, *Katsuwonus pelamis*; BLM = blue marlin, *Makaira nigricans*; BM = black marlin, *M. indica*; SM = striped marlin, *Tetrapturus audax*; SWF = swordfish, *Xiphias gladius*; SBSF = shortbill spearfish, *T. angustirostris*; and SF = sailfish, *Istiophorus platypterus*.

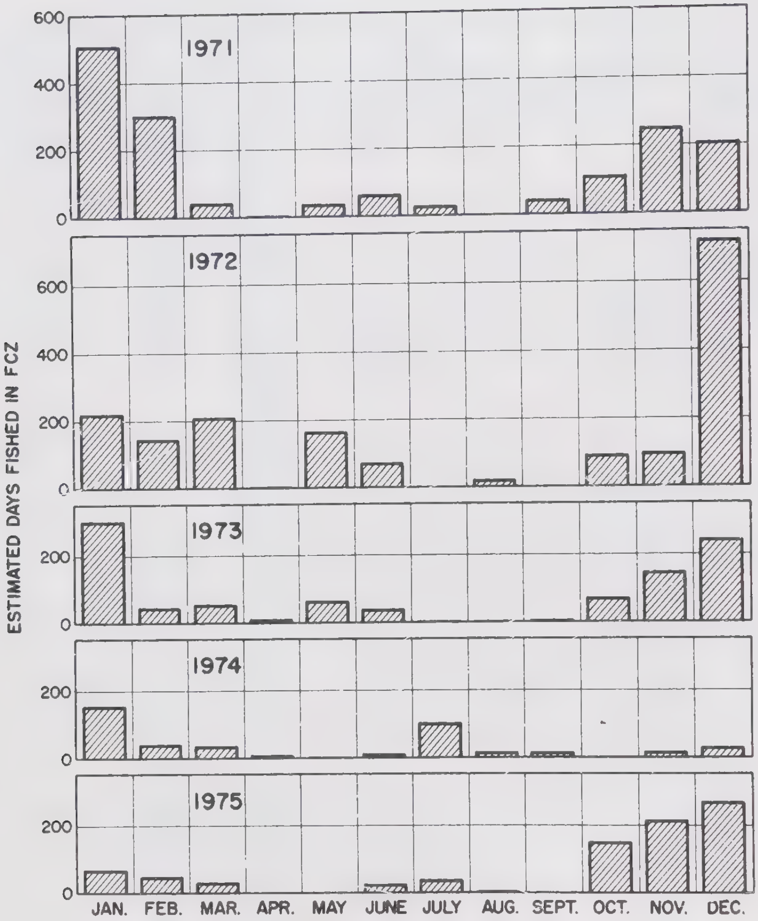

Figure 1. Estimated monthly effort by Japanese longliners within the 200-mile Fishery Conservation Zone of the Northwestern Hawaiian Islands, 1971-75 (Yong and Wetherall, 1980).

TABLE 2. ESTIMATED ANNUAL CATCH (METRIC TONS) OF TUNAS IN THE NORTHWESTERN HAWAIIAN ISLANDS, 1972-77[1]

Year	Albacore	Yellowfin tuna	Bigeye tuna	Bluefin tuna	Skipjack tuna
1972	577	277	1,287	2	2
	26	19	105	26	1,282
	603	296	1,392	28	1,284
1973	348	133	496	2	1
	0	20	109	0	823
	348	153	605	2	824
1974	281	119	95	2	1
	0	50	147	0	1,971
	281	169	242	2	1,972
1975	170	171	512	2	1
	89	167	71	25	1,906
	279	338	583	27	1,907
1976	912	330	1,155	1	1
	0	124	92	0	4,294
	912	454	1,247	1	4,295
1977	480	308	1,514	1	1
	49	337	734	0	4,375
	529	645	2,248	1	4,376

[1] First line is annual catch by foreign longliners.
Second line is annual catch by baitboats.
Third line is total annual catch (line 1 + line 2).

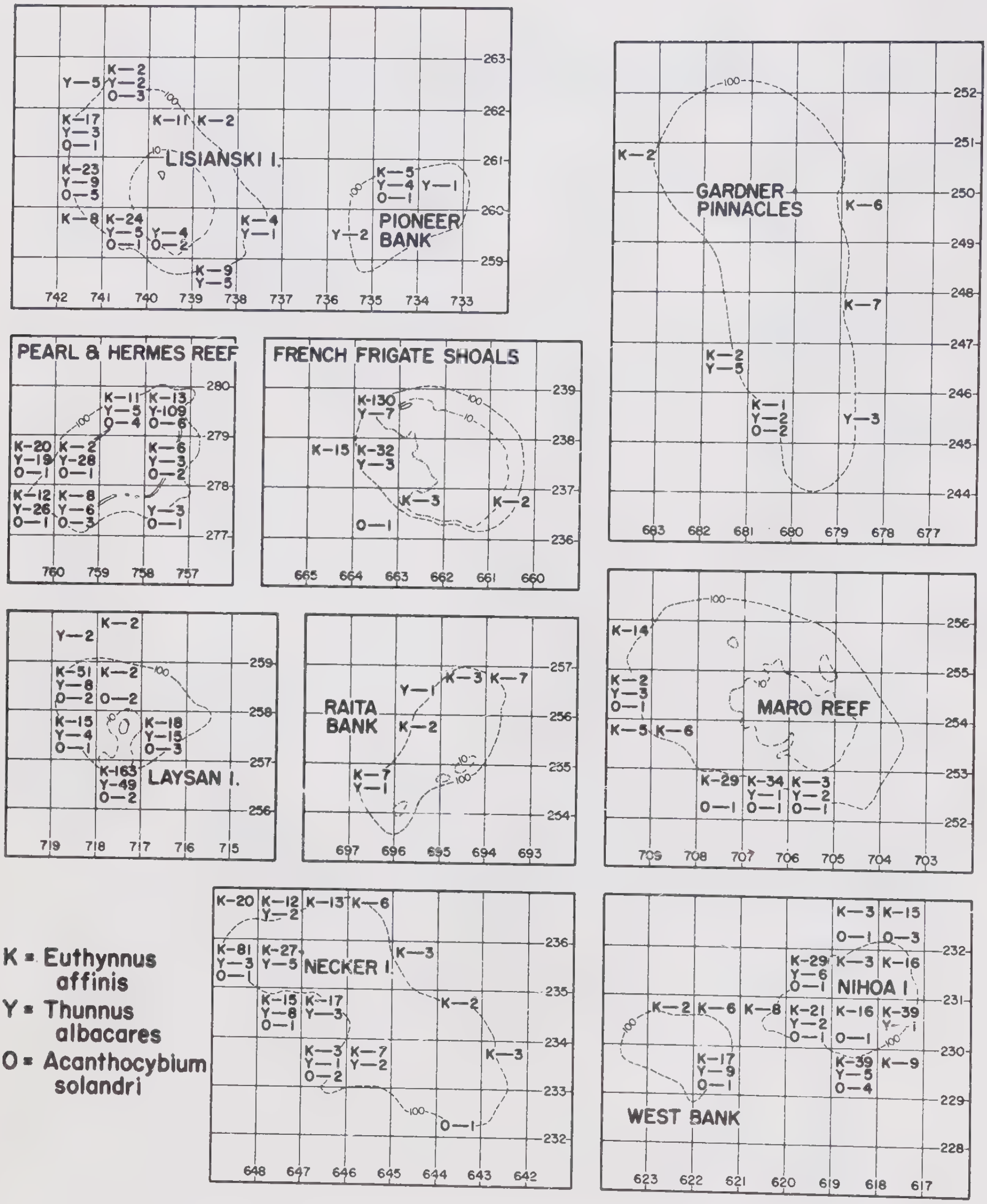
LISIANSKI I.
PIONEER BANK
K—2 Y—2 O—3
Y—5
K—17 Y—3 O—1
K—11
K—2
K—23 Y—9 O—5
K—8
K—24 Y—5 O—1
Y—4 O—2
K—4 Y—1
K—9 Y—5
K—5 Y—4 O—1
Y—1
Y—2
PEARL & HERMES REEF
K—11 Y—5 O—4
K—13 Y-109 O—6
K—20 Y—19 O—1
K—2 Y-28 O—1
K—6 Y—3 O—2
K—12 Y-26 O—1
K—8 Y—6 O—3
Y—3 O—1
FRENCH FRIGATE SHOALS
K-130 Y—7
K—15
K—32 Y—3
K—3
K—2
O—1
GARDNER PINNACLES
K—2
K—6
K—7
K—2 Y—5
K—1 Y—2 O—2
Y—3
Y—2
K—2
K—51 Y—8 O—2
K—2 O—2
K—15 Y—4 O—1
K—18 Y—15 O—3
K—163 Y—49 O—2
LAYSAN I.
RAITA BANK
Y—1
K—3
K—7
K—2
K—7 Y—1
MARO REEF
K—14
K—2 Y—3 O—1
K—5
K—6
K—29 O—1
K—34 Y—1 O—1
K—3 Y—2 O—1
K = Euthynnus affinis
Y = Thunnus albacares
O = Acanthocybium solandri
NECKER I.
K—20
K—12 Y—2
K—13
K—6
K—81 Y—3 O—1
K—27 Y—5
K—3
K—15 Y—8 O—1
K—17 Y—3
K—2
K—3 Y—1 O—2
K—7 Y—2
K—3
O—1
NIHOA I.
WEST BANK
K—3
K—15
O—1
O—3
K—29 Y—6 O—1
K—3
K—16
K—2
K—6
K—8
K—21 Y—2 O—1
K—16 O—1
K—39 Y—1
K—17 Y—9 O—1
K—39 Y—5 O—4
K—9
100
10

Figure 2. Distribution of coastal pelagic fishes in the Northwestern Hawaiian Islands as depicted by the number of fishes caught per cell by trolling, 1976-79

TABLE 3. RELATIVE APPARENT ABUNDANCE OF TROLL-CAUGHT COASTAL PELAGIC FISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

Island/Bank	Effort (Hook/h)	Total Catch (No.)	Catch Rate (No./Hook/h)	No. of Each Species Caught:[1]										
				KK	YF	SJ	WA	DO	RN	BA	C1	C2	C3	BLM
Nihoa	375.2	363	0.97	319	29	4	11	--	--	--	--	--	--	--
Necker	413.4	285	0.69	227	30	10	6	6	2	3	--	1	1	--
French Frigate Shoals	303.1	224	0.74	183	13	19	2	3	1	--	--	3	--	--
Brooks	13.8	7	0.51	7	--	--	--	--	--	--	--	--	--	--
Gardner Pinnacles	200.3	59	0.29	43	10	--	4	1	1	--	--	--	--	--
Raita	12.8	21	1.64	19	2	--	--	--	--	--	--	--	--	--
Maro	241.4	175	0.72	129	3	6	4	7	1	--	10	2	13	--
Laysan	457.1	389	0.85	252	78	18	11	--	2	15	5	5	4	--
Northampton Seamount	99.0	42	0.42	15	15	1	10	--	--	--	--	--	--	1
Pioneer	32.5	24	0.74	6	7	--	3	--	--	--	8	--	--	--
Lisianski	404.7	206	0.51	121	33	6	13	1	--	--	32	--	--	--
Salmon	10.1	6	0.60	1	4	1	--	--	--	--	--	--	--	--
Pearl and Hermes Reef	889.3	379	0.43	77	248	7	18	1	6	--	22	--	--	--
Midway	29.8	2	0.07	--	2	--	--	--	--	--	--	--	--	--
Kure	58.2	1	0.02	--	1	--	--	--	--	--	--	--	--	--

[1] KK = kawakawa; YF = yellowfin tuna; SJ = skipjack tuna; WA = ono; DO = mahimahi; RN = rainbow runner; BA = barracuda, *Sphyraena helleri*; C1 = white ulua, *Caranx ignobilis*; C2 = omilu, *C. melampygus*; C3 = kahala, *Seriola dumerili*; and BLM = blue marlin.

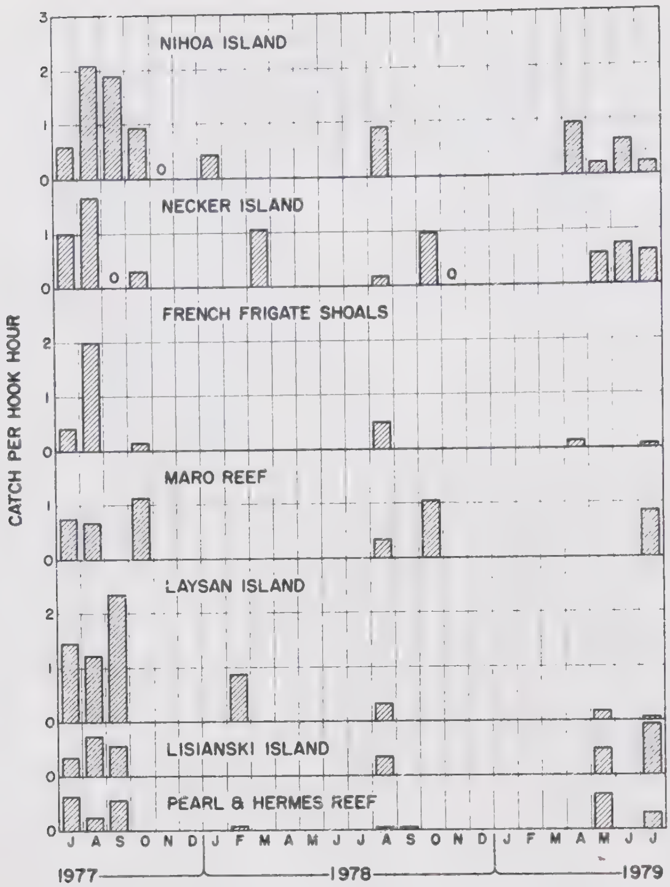

Figure 3. Changes in the catch rate of coastal pelagic fishes with time.

Age and growth

Preliminary von Bertalanffy growth curves were calculated for kawakawa and albacore (Figures 4 and 5).

Fecundity and spawning season

Yellowfin tuna caught on the banks were undeveloped throughout the year. Work to obtain fecundity estimates of ono are presently in progress. Ova development does not appear to be homogeneous within the ono's ovary.

Foraging habits

Over 285 stomach content samples have been collected from troll-caught kawakawa, yellowfin tuna, skipjack tuna, ono, mahimahi, and rainbow runner.

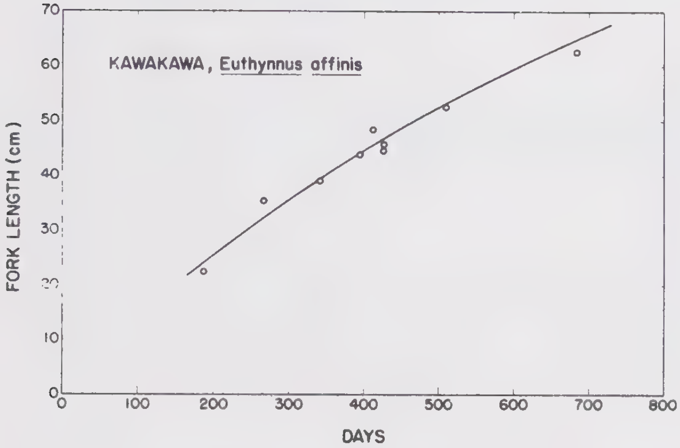

Figure 4. Growth curve of kawakawa from the Northwestern Hawaiian Islands. Von Bertalanffy growth parameters: L_∞ = 117.8 cm, K = 0.42 cm, and T_O = -0.03.

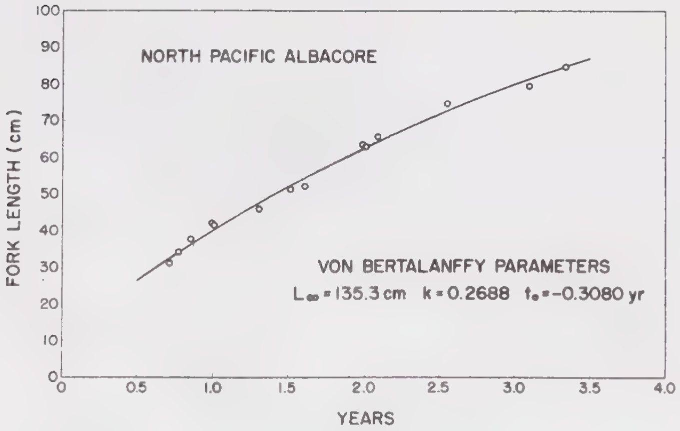

Figure 5. Growth curve of North Pacific albacore

Tagging

Nine-hundred ninety-nine kawakawa, yellowfin tuna, and ono were tagged in 1977. Only a single recovery has been reported, thus far. A yellowfin tuna tagged at Pearl and Hermes Reef was recovered by a Japanese pole-and-line fishing vessel northwest of Pearl and Hermes Reef (lat. 27°40'N, long. 170°30'W). The fish had traveled at least 31 nmi in 37 days.

Night-light stations

Twenty-four night-light stations, mostly during the summer months, have been occupied since 1978. Mackerel scad were attracted to the light at French Frigate Shoals and Kure.

DISCUSSION AND CONCLUSIONS

The catch statistics of foreign longline operations probably provides the best measure of apparent abundance. Estimates of catch and effort by Korean longline vessels operating in the FCZ will also be analyzed in the future.

Because the results are only preliminary no conclusions are made at this time.

FUTURE RESEARCH NEEDS

More fishing effort is needed to observe a change in the relative abundance of the coastal pelagic fishes and to be able to estimate stock size. To determine seasonal availability, more fishing effort is required during the fall, winter, and early spring. Experiments to validate daily growth rings on otoliths have begun for kawakawa and the bigeye scad. Other pelagic species should also be aged. A study of the pelagic squid resource is also needed.

SUMMARY

The relative apparent abundance of longline and troll-caught pelagic species were estimated. Growth curves of _Euthynnus affinis_ and _Thunnus alalunga_ were estimated from daily growth rings on otoliths. Maturation of ovarian ova in ono was nonhomogeneous at the preripe stage.

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Hydrodynamics of suction feeding of fish in motion

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Forward motion was shown to increase the efficiency of suction feeding by causing the ingested volume to be predominantly in front of the fish, instead of being a sphere centred on the fish mouth. This increases the distance from which a prey, located in front of the predator, can be ingested by suction.

A general hydrodynamic model of the external effects of the suction process is presented, showing that this is dependent upon a single non-dimensional parameter, the ratio of a characteristic mouth dimension, divided by the forward swimming speed and the suction time. Data for large-mouth bass, *Micropterus salmoides* show that the observed average forward velocity while feeding, of 3·1 body length/s, serves to increase the ingestion range by more than 60% over suction while not moving.

I. INTRODUCTION

Many teleost fishes feed by means of a sudden enlargement of the buccal and opercular cavities, producing a suction force (Nikolsky, 1963; Alexander, 1967). This suction causes a certain volume to be engulfed and prey capture will take place only if the prey (or at least its centre of gravity) is within this volume. Alexander's (1967) model assumes that the water flow towards the mouth is equal from all directions. This model is applicable mainly to feeding while the fish is motionless. Observations by Nyberg (1971) show that the water swallowed originates mainly in the volume in front of the fish's mouth when the fish is moving while feeding. The present paper describes a quantitative hydrodynamical model for suction feeding while the fish is in motion. Forward motion is shown to increase considerably the range over which food is ingested for a given mouth size and opening rate.

II. THE THEORETICAL MODEL

Suction feeding can be modelled as a hydrodynamic sink (Milne-Thomson, 1968), i.e. a point in space in which fluid is being withdrawn from the ambient surroundings. Essentially, this is the basis for Alexander's (1967, 1969) model of suction feeding. This model, which predicts equal intake from all directions, describes stationary feeding (i.e. when the fish is not moving while feeding) (Alexander, loc. cit.; Elshoud-Oldenhave & Osse, 1976). However, the symmetry required by this model breaks down when the predator is moving while the feeding process takes place and fluid is ingested preferentially from the forward direction (Nyberg, 1971). This enables more efficient feeding as the volume of water in which the prey has to be located is distended in the forward direction.

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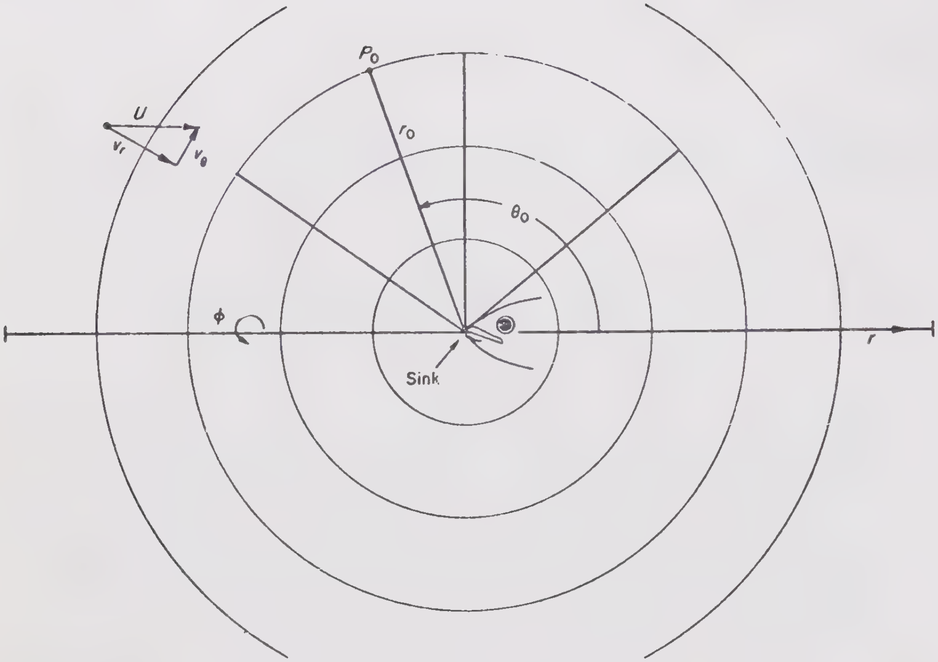

FIG. 1. Definition of the spherical coordinate system moving with the fish. r_0 and θ_0 are the coordinates of point P_0 and v_r, v_θ are the radial and tangential components of the oncoming velocity (which is equal and opposite to the fish velocity).

In order to describe this process mathematically we define a spherical coordinate system attached to the centre of the predator's mouth, which will serve as the sink point (Fig. 1). Thus, any motion of the fish as a whole will be described by a velocity, U, of the surrounding fluid. This velocity can be constant, or time dependent (acceleration) and is in a direction opposite to the movement of the fish's centre of mass. We assume that the direction of motion of the fish is constant, i.e. it is swimming in a straight line while feeding takes place. This limitation could easily be relaxed but as most suction feeding takes place in less than one-tenth of a second, it is probably a realistic assumption.

The velocity field induced in an incompressible fluid (water) by a point sink is (Milne-Thomson, 1968):

$$v_r = -\frac{Q}{4\pi r^2}; \; v_\theta, v_\phi = 0 \qquad (1)$$

where v_r is the radial component (the minus sign indicates inward flow), r is the distance from the sink, Q is the rate of mass intake, and θ and ϕ are defined in Fig. 1. As mentioned above, any forward speed of the fish is translated into water motion, so that the velocity components due to this motion are, from Fig. 1 (assuming axial symmetry):

$$V_r = U\cos\theta; \; v_\theta = -U\sin\theta \qquad (2)$$

and the total velocity at each point is obtained by superposition of the two fields:

$$v_r = U\left(\cos\theta - \frac{Q}{4\pi U r^2}\right) \qquad (3a)$$

$$v_\theta = -U\sin\theta. \qquad (3b)$$

We now calculate the time, T, it takes for the mouth cavity to fill. This is obtained from:

$$N = \int_{0}^{T} Q \, \mathrm{d}t \tag{4}$$

where N is the change in mouth volume obtained by the feeding action. For the cases observed (Alexander, 1969; Nyberg, 1971) the rate of water intake Q is essentially constant. This enables a simple solution to the integral equation (4), so that:

$$T = N/Q. \tag{5}$$

The trajectories of different points in the water mass are now calculated by integrating the velocities. This is done numerically by defining a starting point $P_0(r_0, \theta_0)$ at which the particle considered is positioned when the suction process starts, i.e., $t=0$. The velocity induced by point P_0 is then found by equation (3). Taking a very short time interval, Δt, the position P_1 (r_1, θ_1) of the particle initially at P is obtained by:

$$r_1 = r_0 + (v_r)_0 \, \Delta t \tag{6a}$$

$$\theta_1 = \theta_0 + (v_\theta)_0 \, \Delta t. \tag{6b}$$

This step is repeated a large number of times so that the trajectory of particles originating at each point is found. The calculation for a given initial point was terminated when the trajectory approached within a very small distance from the origin, which indicates ingestion. At the origin $r=0$ the radial velocity becomes infinite, which causes numerical difficulties, so that a very small distance (10^{-5} cm) was chosen, after checks for accuracy. The computation was also terminated for a given point when a comparison of the coordinates at two successive time-steps during the interative process showed the distance from the origin increasing, i.e. the particle was moving away from the sink. This indicates that the particle would not be ingested.

The calculations were carried out on a Tektronix mini-computer. Various initial points P_0 were selected for given values of Q and U and their trajectories calculated after the suction process began. The time step was chosen as $\Delta t = 0{\cdot}0001$ [s], after testing to see that further reducing the time step did no longer noticeably affect results. When a particle reached a point within the minimum radius $r_m = 10^{-5}$ [cm] mentioned before, the initial coordinates and the time elapsed was recorded. A map of initial positions for particles finally ingested, and the time it takes for them to reach the sink was obtained.

III. RESULTS AND DISCUSSION

We can distinguish three cases: (i) initial positions where particles never reach the sink as they are swept away faster than being pulled towards the mouth. This case does not exist for the stationary suction feeder, (ii) particles which end up at the origin, but the time it takes them to get there is longer than the time, T, it takes to fill the mouth cavity so that they are not included, and (iii) particles that arrive at the mouth opening in times less than T, and are ingested.

We first examine category (i) which describes the region from which prey particles will always escape. This can be found by inspection of equation (3a). For a particle to escape the radial velocity has to be positive at some point of its trajectory. This condition is written as:

$$\cos\theta \geqslant \frac{Q}{4\pi U r^2}$$

defining a new parameter K as:

$$K = \frac{Q}{4\pi U}$$

the escape condition becomes:

$$\cos\theta \geqslant \frac{K}{r^2} \tag{7}$$

which gives, for known Q and U, a relation between distance and angle for escaping particles. Equation (7) indicates that the 'escape' zone includes only points to the rear of the sink. Particles which are in such positions when suction starts are never ingested. This region includes the area to the left of the broken lines in Fig. 2 each of which stands for a different value of K, which is a measure of the ratio of mouth cavity opening rate to forward swimming speed. For a given fish (with known opercular and buccal volume change rate) increasing K stands for decreasing forward velocity while feeding. $K \to \infty$ is the case of a non-moving fish described by Alexander (1967, 1969).

The broken lines on Fig. 2 are the limits of the initial escape zone. Prey anywhere in this zone (which is defined by $\cos\theta_0 \geqslant \frac{K}{r_0^2}$) will never move towards the sink and never be in any danger of ingestion. The full lines indicate the actual limits of the region which can be ingested. The volume between the dotted and full lines for any given K define a region where prey is initially attracted to the mouth by suction, but at some intermediate time

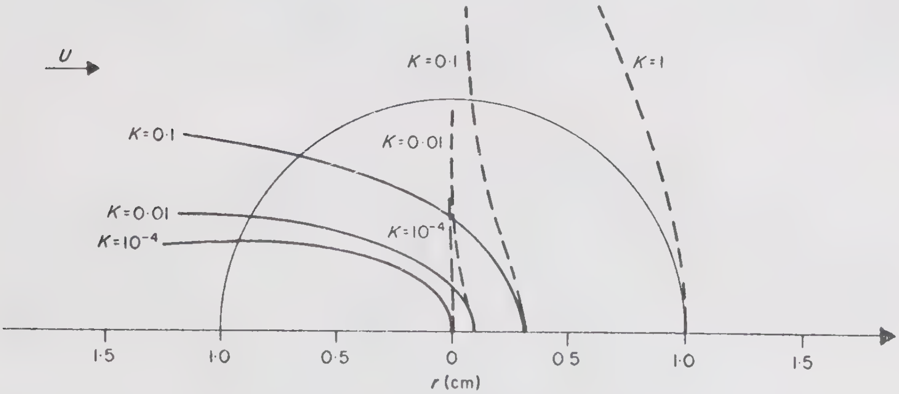

FIG. 2. Limits of capture area for various values of the capture parameter K. The broken lines indicate the limits of the escape zone defined in equation (7). Points in the area between the solid and the broken line for a given value of K initially approach the sink but finally escape. Only points to the right of the full lines are ingested. The unit circle is also given for orientation purposes.

is swept off. This change takes place when the particle moves beyond the broken line, at any time during its trajectory.

Actual measurements of all the parameters required for equations (3–5) were found for only one case, that of large-mouth bass, *Micropterus salmoides* (Nyberg, 1971). These are now used to calculate the shape of the feeding volume of this species. The data used is from Nyberg (1971: fig. 3 and data for bass number 4). This was 14 cm long and moving at an average speed of 3·1 body-lengths/s, i.e. at a speed of $\simeq$43 cm/s. The mouth volume change is 5·2 cm^3, this occurring with $T = 0{\cdot}02$ s. The rate of intake is therefore $Q = 250$ cm^3 s^{-1} and:

$$K = \frac{250}{4 \times \pi \times 43} = 0{\cdot}46 \text{ cm}^2 \tag{8}$$

to two significant figures. Figure 3 shows the volume of water taken in during the feeding process. The centre of mass of the prey has to be within this volume to be caught. The sphere of equal volume appears on this figure or a broken line for comparison, showing the increase in forward feeding range due to the forward motion of the fish. The radius of the sphere mentioned, which indicates the volume ingested by a non-moving fish, is 1·07 cm while the maximum forward dimension of the feeding volume is ~1·73 cm, i.e. the maximum capture distance is increased by over 60% in this case.

The volume indicated in Fig. 3 was found by searching for the points which would be captured by the source within time $T = 0{\cdot}02$ s, starting from initial positions in various directions. This calculation has to be corrected slightly for the effect of the bass head, which defines a region of no intake (shaded area in Fig. 3). This displaced volume is obtained by:

$$N_{\text{head}} = \int_{-\phi_h}^{\phi_h} \int_{-\theta_h}^{\theta_h} \int_{0}^{R_h} r^2 \sin\theta \, dr \, d\theta \, d\phi \tag{9}$$

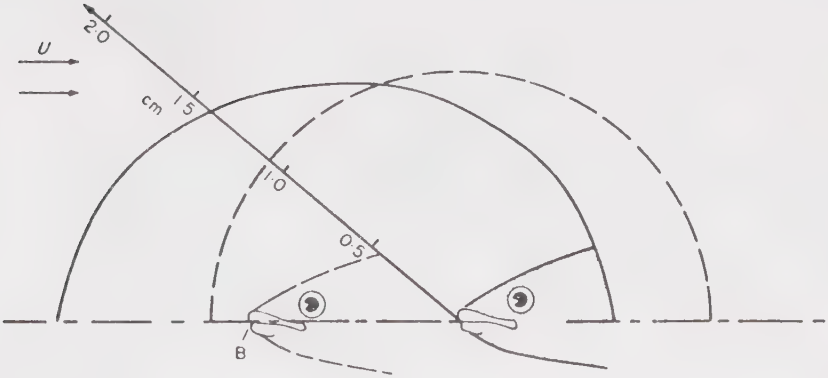

FIG. 3. The capture area (full line) of a large-mouth bass described by Nyberg (1971), the broken circle indicates the ingested volume of a stationary fish. Point B indicates the fish's position at the end of the suction process.

where R_h is the radius of the shaded volume and θ_h, ϕ_h are the angular half-depth, and half-width of the head. The radius is essentially constant over the included head area $0{\cdot}65 < R_h < 0{\cdot}68$ cm, and with $\theta_h \simeq 30°$ and $\phi_h \simeq 15°$ (Trautman, 1957) gives a volume $N_h \simeq 0{\cdot}05$ cm^3, which is less than 1% of the total volume engulfed. Including this negligible correction moves the most forward point by 0·015 cm outwards, and can therefore not be shown clearly on Fig. 3.

The accuracy of the calculations above was checked by means of a numerical integration of the contour of the body of revolution in Fig. 3. A 16-point Simpson's rule integration gave a total volume of 5·185 cm^3, i.e. an error of less than 0·3%.

Nyberg's statement that particles were not observed flowing forward can now be quantitatively compared by obtaining the volume of fluid swallowed, which was initially at angles θ of less than 90°. Again by numerical integration, this is 0·97 cm^3. Subtracting the volume displaced by the fish head (= 0·05 cm^2), we see that only $0{\cdot}92/5{\cdot}2 = 18\%$ of the total volume swallowed originates from behind the tip of the fish's nose. This value can be compared to ≃50% originating from the area behind the fish nose in static feeding. In most cases, prey will not be in this region so that a reduction by a factor of 3 in the intake of unwanted volume is achieved. Also, the speeds in the rear zone are lower, so that heavy particles such as the dirt observed by Nyberg would be moved even less, as there is a delay in getting them moving.

Some particle trajectories appear in Fig. 4. These trajectories are obtained by the technique described before, by plotting the instantaneous position at each time step. Here it was assumed that the particles were neutrally buoyant and relatively small (compared to a typical dimension of the problem—the mouth diameter). Bigger, or non neutrally-buoyant prey would be displaced somewhat less in the same time. When a particle is of different density than water, an additional drag force must act on it, to counteract the body force. This drag can

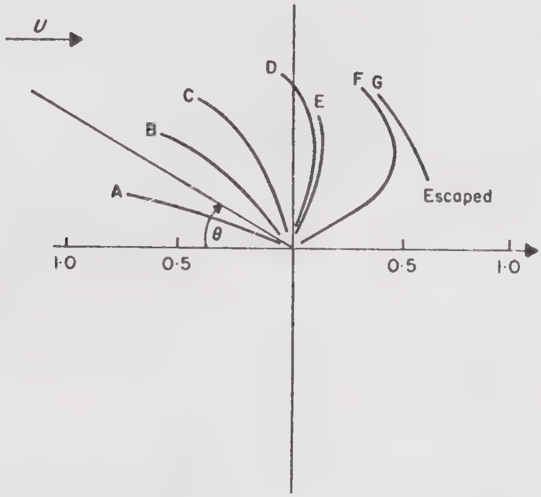

FIG. 4. Particle trajectories for the large mouth bass of Fig. 3.

only be produced by means of a velocity difference between the particle and the surrounding water so that the particle would move a shorter distance in a given time. When prey size is large, different parts of it are moved at different speeds due to the velocity field (3) so that rotation, and similar processes occur at the expense of kinetic energy so that again, the prey moves more slowly.

Heavy particles would also be subject to inertia so that when following a trajectory like F (Fig. 4) it would not be able to follow the sharp curvature and might escape. The ' ingestion volume ' shown in Fig. 3 is therefore an upper limit, with real feeding distances expected to be somewhat smaller (for both motionless and swimming suction).

It would be of interest to compare the present predictions with further data on various fish species feeding by suction. A more quantitative check would then be possible, testing the influence of the parameter K (ratio of rate of mouth volume change to forward swimming speed) by comparing captures by individuals of the same species at different sizes, and swimming speeds. The ratio K can be completely non-dimensionalized by dividing by a length parameter (squared). This would probably help collapse experimental data more neatly, especially when data from individuals of greatly varying sizes are compared, thereby generalizing the model. The length-related quantity in K is the change in volume of the mouth N, which has dimensions of length cubed. The squared length required to non-dimensionalize K is therefore $N^{2/3}$. The non-dimensional suction number S is then:

$$S = \frac{Q}{4\pi U N^{2/3}} \tag{10}$$

and substituting $Q = N/T$ we obtain:

$$S = \frac{N^{1/3}}{4\pi U T} \tag{11}$$

Defining the characteristic length dimension of the mouth as $D = N^{1/3}/4\pi$ (related to an average mouth cavity radius) we obtain finally for the nondimensional suction number S:

$$S = \frac{D}{UT} \tag{12}$$

The appropriate nondimensional length parameter is then $r = r/D$. Figure 5 shows an application of these nondimensional coordinates. The ratio of ingestion distances directly forward to that in the opposite direction, L is shown as a function of S. When $S \rightarrow \infty$, i.e. the case of $U = 0$ (nonmoving predator), this ratio $L = 1$ as the ingestion distance in all directions is equal. For the large-mouth bass shown in Fig. 3 we have from equation (11):

$$S = \frac{5{\cdot}2^{1/3}}{4 \times \pi \times 43\ 0{\cdot}02} = 0{\cdot}16. \tag{13}$$

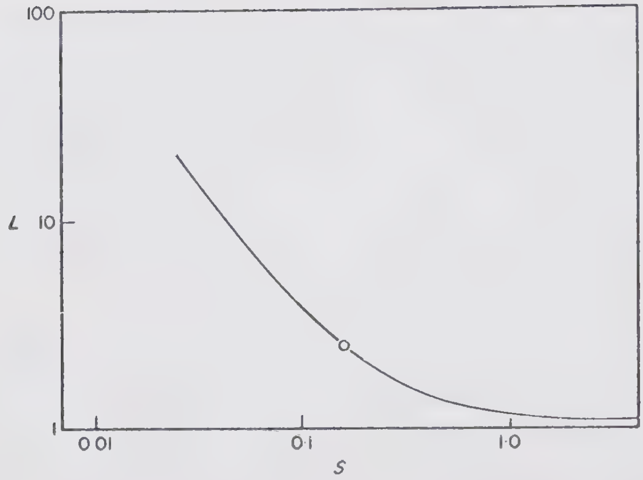

FIG. 5. The ratio of ingestion distance directly forward, and directly behind the fish's mouth L as a function of the generalized suction number S (characteristic mouth size divided by forward speed and suction time). The circle shows experimental data for large mouth bass (Nyberg, 1971).

In this case $L = 2{\cdot}55$ (Fig. 5). Finally, as the forward speed grows for given suction rate, $L \rightarrow \infty$ while $S \rightarrow 0$. The ratio L is a measure of the efficiency of directed suction feeding, as prey will usually be in front of the predatory when the feeding starts. Large L indicates a small proportion of water ingested from behind the head, i.e. the wasted volume is smaller.

The advantage of having Fig. 5 as a function of S is that otherwise there would be a separate curve for each mouth size N. We see that forward swimming has no significant influence on the capture distance when $S > 0{\cdot}5$. When S is smaller, the slope of the curve starts going up more rapidly indicating growing advantage of forward swimming in terms of directed suction. This leads to the conclusion that only rapid swimming is worthwhile for suction feeding as slow swimming does not much increase the forward bias of the capture volume. Also, any further increase in speed just before suction shifts the curve to the left, i.e. to still higher L. This might explain the observation (Nyberg, 1971) of a last minute increase in velocity of the predator, when hunting mobile, midwater prey (minnows). For the 14 cm large-mouth bass, with a feeding volume of $5{\cdot}2$ cm^3, $S = 0{\cdot}5$ is equivalent to a speed of *c.* 14 cm, i.e. one body-length/s. This is just slightly less than the optimum cruising speed (Weihs, 1977). The high swimming speed observed while feeding, which is much more costly energetically, must therefore have a different reason. This is possibly the increased forward capture distance.

An interesting conclusion, from the functional form of the suction number S is that larger fish (which presumably will have larger mouth cavities) have to move at higher speeds to get the same advantage in suction feeding as smaller predators. Taking equal mouth cavity opening times T, the required increase in speed grows linearly with fish size (assuming geometric similarity between fish of differing size). Swimming speed, however, grows in less than linear relation to size so that smaller predators will be able to make better, and more efficient use of suction feeding. This conclusion was also reached by Nyberg (1971) through a different line of arguments, after he observed higher capture rates by suction by the smaller individuals.

This study was made while I was a NRC-NOAA Senior Research Associate. I thank Drs J. R. Hunter and R. Lasker for their hospitality and encouragement.

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ENERGETIC SIGNIFICANCE OF CHANGES IN SWIMMING MODES DURING GROWTH OF LARVAL ANCHOVY, *ENGRAULIS MORDAX*

DANIEL WEIHS[1]

ABSTRACT

The swimming behavior of larval northern anchovy, *Engraulis mordax*, in the first few days after hatching is different from the intermittent beat-and-glide mode used by older larvae and later stage fish. It is shown mathematically that the bursts of continuous swimming typical of these yolk-sac larvae is the more efficient form of locomotion at this stage, because of their small size. This advantage changes as the larva grows out of the size range in which water viscosity is the dominant factor (small Reynolds number). When the larva reaches a length of 5 mm, typical Reynolds numbers are such that intermittent swimming gradually becomes the more economical mode, and this mode is dominant when the larvae reach 15 mm. These analytical results compare well with observed behavioral changes.

Swimming behavior of the northern anchovy, *Engraulis mordax*, changes dramatically during growth in the larval stage (Hunter 1972). At hatching, the motion of yolk-sac larvae consists of bouts of continuous, very energetic swimming. This behavior persists for the first 3-4 days of growth, changing to beat-and-glide swimming at the close of the yolk-sac period. The beat-and-glide mode is then retained during the rest of the fish's life.

Intermittent swimming, or beat and glide, is an efficient mode of locomotion for adult fish, enabling increases by a factor of two or more in the range achieved for a given energy expenditure (Weihs 1974). The problem addressed in the present paper is whether the changes in swimming behavior mentioned above also have an energy-saving function. The energetic advantage of intermittent swimming may not exist during the early life stages of fishes because of the importance of viscous effects on small organisms. This study includes setting up a theoretical framework for the analysis of energetics of swimming during the various stages of the fish's life history. The forces and energy required for swimming in the continuous and intermittent modes are then calculated and compared at different stages of larval development. These stages are hydrodynamically distinguished by the nondimensional Reynolds number, Re, which is a function of both length and speed. The value of the Re defines the relative importance of viscous and inertial effects on the hydrodynamic resistance to motion.

THEORETICAL MODEL

Consider a fish swimming in a straight line at constant depth. We shall assume the fish to be neutrally buoyant so that the only forces acting are in the horizontal plane. Fish of negative buoyancy can be included in the following analysis by equating the excess weight of the fish in water (which is usually not more than 6% of its weight in air) and lift forces produced on the body and fins. However, this is not directly relevant to the present discussion as these forces are perpendicular to the plane of motion, and shall therefore be left out for simplicity.

Returning to the horizontal plane, the forces acting are the thrust applied by the fish, T, and the drag on the fish, D, acting in the opposite direction. The drag is a combination of viscous drag due to friction and form drag, which also is an indirect result of the friction caused by areas over which the flow is separated from the fish body. The drag force can be written (Hoerner 1965) as

$$D = \frac{1}{2} \rho A C_D u^2 \qquad (1)$$

where ρ is the water density; A the frontal area (seen in frontal projection); C_D a nondimensional drag coefficient dependent on shape, roughness, and other factors to be discussed below; and u the relative velocity between the fish and the water

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some distance away, which is not disturbed by the fish's passage.

The drag coefficient C_D has been found experimentally to be a similar function of Re for various shapes. Thus, for all shapes tested (Hoerner 1965, chapter 3), the coefficient C_D is a decreasing function up to Re 200-300, being a constant for larger Re up to the turbulent regime which starts at about Re = 500,000, where a new, lower, constant value is obtained. Thus when Re>200, hydrodynamic drag becomes proportional to the velocity squared, as the other factors in Equation (1) do not change for a fixed body.

The Re>200 regime was examined by the author (Weihs 1974) previously and will therefore be mentioned here for comparisons only. When Re<200, two main regimes are observed, that of Re<10 and 10<Re<200. The low Re range, in which velocity plays a much more important role than the inertial (acceleration) force effects, has $C_D \propto \mathrm{Re}^{-1}$. Strictly speaking, this regime ends when Re = 1, but experiments have shown that this relationship can be applied up to Re = 10 with good accuracy. Vlymen (1974) actually used this relationship at Re = 30, where C_D, estimated by the low Re formula, still is within 10% of the exact value, for his analysis of larval anchovy swimming. The remaining range is a transition regime where C_D gradually changes from the low Re form to the high Re ($C_D \propto \mathrm{Re}^0$) form.

As continuous swimming in anchovy larvae is observed mainly in the yolk-sac stage (2.8-5 mm long), the low Re regime is relevant. Thus, Re = 8 corresponds to a 3 mm long larva moving at 3 mm/s, and a 5 mm long larva, moving at 5 mm/s, experiences a Re<30.

Applying the relationship for low Re ($C_D \propto \mathrm{Re}^{-1}$), Equation (1) can be written

$$D = \frac{1}{2}\rho ACu \qquad (2)$$

where C is a numerical constant depending on the shape.

When a fish is actively swimming by means of body and fin oscillations, the drag force is affected, both through the increase in frontal area A, and through the change in the numerical coefficient C. Thus, for example, $C = 20.37$ for a disc moving in a direction normal to its plane, and is equal to 13.6 when moving parallel to its plane. Experimental data collected by Webb (1975) show that the drag coefficient for fish swimming at high Re can be up to four times that of a rigidly gliding fish. For the low Re regime considered here, the increase in drag coefficient caused by swimming motions does not exceed a factor of 2, for a long slender body (Wu et al. 1975). This increase is written as

$$D_s = \frac{1}{2}\rho AC\alpha u \equiv \alpha Ku \qquad (3)$$

where α is the ratio of swimming to gliding drag and the subscript s stands for active swimming. The equation of motion for fish, while actively producing a thrust T is

$$T = m\frac{du}{dt} + \alpha Ku \qquad (4)$$

where m is the fish mass (slightly augmented by the added mass at higher Re), and K is defined in Equation (3).

The energy (E) required to traverse a distance L within time τ is

$$E = \int_0^\tau T\,u\,dt. \qquad (5)$$

There is no available information on the dependence of propulsive efficiency on swimming speed for larval anchovy, so that we have to perform the calculations on the energy required, and not the energy actually expended by the fish. However, for comparison of different swimming modes, these are equally applicable.

The purpose of the present study is to compare the effectiveness of continuous and intermittent swimming of larval fish so that we start by finding the energy, E_c, required for swimming at constant speed U_c over the same distance L. From Equation (5),

$$E_c = T_c U_c \tau = T_c L \qquad (6)$$

where the subscript c stands for continuous swimming. Defining the energy expenditure per unit distance as $\bar{E} = E/L$ we obtain, by applying also Equation (4),

$$\bar{E}_c = T_c = \alpha KU_c. \qquad (7)$$

Intermittent swimming, on the other hand, requires energy only during the beating part of the cycle so that the total energy for one beat-and-glide cycle is described by

$$E_v = \int_0^{t_1} T\,u\,dt = \int_0^{t_1}\left(mu\frac{du}{dt} + \alpha Ku^2\right)dt \qquad (8)$$

where t_1 is the time spent in active swimming during the cycle. In order to integrate Equation (8) we have to obtain the functional dependence of u on the time t. This is done with the aid of Equation (4). Taking the thrust applied to be constant (T_0), Equation (4) can be solved in closed and general form. It was previously shown (Weihs 1974) that constant thrust production is the most efficient procedure so that we can use this assumption here, recognizing that any other behavior will probably be more wasteful in terms of energy. After some rearrangement, Equation (4) is

$$\frac{du}{dt} + \frac{\alpha K}{m} u - \frac{T_0}{m} = 0 \tag{9}$$

with boundary condition

$$u = U_i \text{ at } t = 0 \tag{10}$$

where U_i is the initial velocity at the beginning of the beat phase, which is equal to the speed at the end of the gliding phase. The solution is

$$u = (U_i - U_0) \exp\left(-\frac{\alpha K}{m} t\right) + U_0 \tag{11}$$

where $U_0 = T_0/K$ is the final velocity which the larva would attain if the beating phase were sustained for a long enough period. U_0 is higher than the final speed actually obtained during the beat phase U_f. Substituting Equation (11) into Equation (8) and integrating, recalling that the speed at t_1 is U_f, we have

$$E_v = mU_0 (U_0 - U_f) + \alpha K U_0{}^2 t_1. \tag{12}$$

To find t_1, we substitute U_f in Equation (11) with $t = t_1$ and obtain, after algebraic reduction

$$t_1 = \frac{m}{\alpha K} \ln \frac{U_0 - U_i}{U_0 - U_f} \tag{13}$$

so that the energy required during one beat-and-glide cycle is

$$E_v = mU_0{}^2 \left[\left(1 - \frac{U_f}{U_0}\right) + \ln \frac{1 - \frac{U_i}{U_0}}{1 - \frac{U_f}{U_0}} \right]. \tag{14}$$

The energy per unit distance crossed during one cycle in intermittent swimming is

$$\bar{E}_v = \frac{E_v}{l_1 + l_2} = \frac{E_v}{U_i \tau} = \frac{E_v}{U_i (t_1 + t_2)} \tag{15}$$

where l_1, and l_2 are the distances crossed during beating and gliding phases, respectively. The sum of l_1 and l_2 is taken to be equal to the continuous swimming speed U_c multiplied by the total cycle time, as we compare energy required for crossing the same distance $l_1 + l_2$. Thus, U_c is also the average velocity during the whole intermittent swimming cycle

$$U_c = \frac{l_1 + l_2}{t_1 + t_2} \tag{16}$$

To compare energy expenditure in intermittent and continuous swimming, we define a ratio S

$$S = \frac{\bar{E}_v}{\bar{E}_c} = \frac{E_v}{\alpha K U_c{}^2 (t_1 + t_2)} = \frac{E_v (t_1 + t_2)}{\alpha K (l_1 + l_2)^2} \tag{17}$$

Intermittent swimming is more efficient only when the numerical value of S is less than unity. To calculate values of S we need explicit expressions for l_1, l_2, t_1, and t_2. The beat phase velocity has already been found, Equation (11), so that l_1 is easily obtained by integration, using t_1, Equation (13), as the upper bound

$$l_1 = \frac{m}{\alpha K} \left[U_0 \ln \frac{U_0 - U_i}{U_0 - U_f} - (U_f - U_i) \right]. \tag{18}$$

The gliding phase of intermittent swimming is described by

$$m \frac{du}{dt} + Ku = 0 \tag{19}$$

which is obtained from Equation (4) when no thrust is applied, and gliding drag is experienced by the fish. The relevant initial condition is

$$u = U_f \text{ when } t = 0 \tag{20}$$

and the speed is

$$U = U_f \exp\left(-\frac{K}{m} t\right) \tag{21}$$

with the time spent gliding t_2 obtained from the fact that at t_2 the speed is back to U_i. After some reshuffling

$$t_2 = \frac{m}{K} \ln \frac{U_f}{U_i}. \qquad (22)$$

Integrating Equation 20 gives l_2

$$l_2 = \int_0^{t_2} U_f \exp\left(-\frac{K}{m}t\right)dt = \frac{m}{K}(U_f - U_i). \qquad (23)$$

To nondimensionalize, we now divide all velocities by U_0. Substituting Equations (13), (14), (18), (22), and (23) into S (Equation (17)) and simplifying results in

$$S = \frac{\left[(1-\bar{U}_f) + \ln\frac{1-\bar{U}_i}{1-\bar{U}_f}\right]\left[\ln\frac{1-\bar{U}_i}{1-\bar{U}_f} + \alpha\ln\frac{\bar{U}_f}{\bar{U}_i}\right]}{\left[(\alpha-1)(\bar{U}_f-\bar{U}_i) + \ln\frac{1-\bar{U}_i}{1-\bar{U}_f}\right]^2} \qquad (24)$$

where the line over the speeds signifies values divided by U_0. The ratio S serves now as a quantitative criterion, showing which mode of swimming is more efficient. The advantages of the comparison approach are now clear, as the only parameter specific to the fish is α which, as mentioned before, can vary between 1 and 2 only. All other factors, such as fish mass, frontal area, and the numerical coefficient of drag, have cancelled out, dropping many of the uncertainties of such calculations.

Results and Discussion

Equation (24) is now studied for various values of the parameters involved. As mentioned before, the numerical value of S indicates the relative efficiency of intermittent and steady swimming. When $S>1$ beat-and-glide swimming is more costly. The three variables appearing in S are bounded by well-defined limits, which makes the parametric study of Equation (24) easier. The nondimensional "final" velocity, at the end of the beat phase, is limited by $0<\bar{U}_f<1$ as U_0 is the highest velocity obtainable by the animal (see Equation (11)) under present conditions. By definition, $0<\bar{U}_i<\bar{U}_f$. The yolk-sac larvae and later stage larvae are combinations of elongated and round shapes so that the limits of α are $1 \leq \alpha \leq 2$. The range of values of α is obtained from the fact that for elongated (fish) bodies, the ratio of drag in normal motion to resistance to tangential relative motion does not exceed 2 in the viscous domain. Only some sections of the fish bodies are in pure normal motion (perpendicular to the local flow direction), consequently the average ratio is always <2.

It is also clear that the larger the numerical value of α, the larger the possible gains by means of intermittent swimming, because the drag when actively swimming is proportionally greater than while gliding so that breaks in the swimming phase will be more advantageous. Therefore, we first take $\alpha = 2$ as a reasonable upper limit. Figure 1 shows the results of such calculations. The coordinates are the energy ratio S versus the normalized average velocity U_c. The calculations were performed for different values of the final

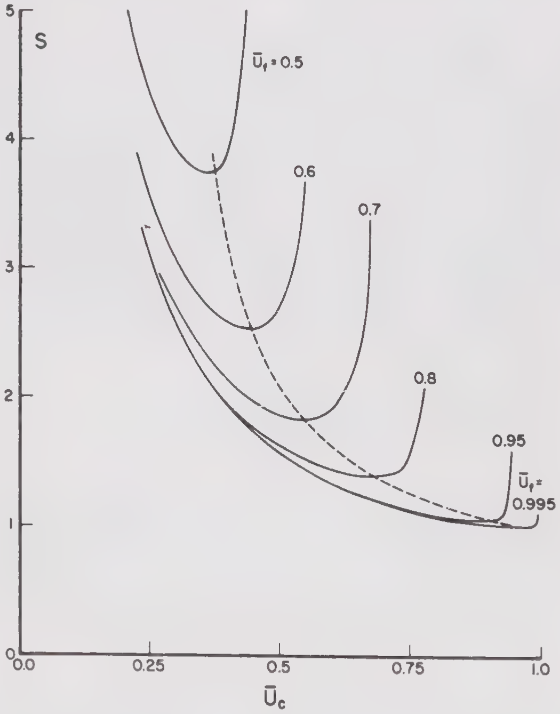

FIGURE 1.—The ratio of energy required per unit distance S for intermittent swimming and continuous swimming respectively, versus the nondimensional average speed $\bar{U}_c$, for various values of speed at the end of the beating phase, $\bar{U}_f$. All speeds are normalized by the speed U_0 attained at maximum sustained thrust T after a long time. Dashed line shows locus of minimal energy ratio at different $\bar{U}_f$. Ratio of swimming to gliding drag α = 2.

velocity U_f, varying the initial velocity U_i to obtain different average speeds.

The main result of this Figure is that S is always >1, i.e., for the speeds and sizes at which viscous effects dominate continuous swimming is always more efficient. This calculation is based on the relation $C_D \propto \mathrm{Re}^{-1}$ and is therefore valid for Re up to 10. Larval anchovy tend to swim at speeds of about 0.8 body length/s (Hunter 1972) when swimming intermittently. Thus the Re typical of 3-day-old larvae whose length (Zweifel and Hunter[2]) is about 4 mm at 18° C is also about 10. At age 3 days, larvae spent <20% of the time swimming intermittently, but 2 days later (Hunter 1972, fig. 1) about 90% of the time is spent in beat-and-glide motion. This level of intermittent swimming is retained thereafter. This sharp change coincides with the time the animal "grows out" of the viscous regime (the Re is essentially proportional to fish length squared), e.g., when the larvae is 5 mm long, the Re is 20.

Recalling that at high Re, beat-and-glide swimming is the more efficient motion (Weihs 1974), the energy saving obtained is probably one of the reasons for the observed change in swimming behavior.

The fact that the average continuous speeds are much higher also results in savings of energy. For a 3-4 mm long larva, swimming at over 1 cm/s brings it again to Re of over 20, so that the drag coefficient is smaller, and some coasting at the end of the bout of continuous swimming is possible. At lower Re, in the purely viscous regime, no coasting is possible as the inertial effects are negligible and motion ceases immediately when oscillations stop. It is therefore advantageous for the fish, for hydrodynamic reasons, to swim continuously during the first few days of the larval phase, changing to beat-and-glide swimming later on. It should be noted here that the present calculations and data are for a water temperature of 17°-18° C. Both viscosity of water and the growth rate of larvae (see footnote 2) depend on the temperature, so that data collected under different ambient conditions might lead to a later (or earlier, if the temperature is higher) change of swimming mode.

Further examination of Figure 1 shows that for each terminal velocity in the beating stage there is a value of $\bar{U}_c$ for which the ratio S attains a minimum (marked by the dashed line). The value of this minimum approaches unity and the curves become more shallow as $\bar{U}_f$ increases. Thus, if an anchovy larva swims intermittently at low Re, it should do so at high average speeds, so that the energy penalties incurred due to swimming in the beat-and-glide mode are minimal.

Figure 1 also shows that the lowest penalties for using intermittent swimming are obtained when $\bar{U}_f$ approaches unity, for the whole range of average speeds. Therefore, the value $\bar{U}_f = 0.995$ was chosen for calculations of the effect of varying α (the ratio of swimming to coasting drag). These appear in Figure 2, where the dependence of S on $\bar{U}_c$ is shown. The range of values of α to be expected in nature is described by the shaded area, showing as expected that the smaller the α the more advantageous is continuous swimming. When $\alpha > 2$, which can only happen at higher Re, a range of values of $\bar{U}_c$ and $\bar{U}_f$ exists where S is smaller than unity, i.e., intermittent swimming is more efficient. This is shown by the dashed curve on Figure 2 where for $\bar{U}_f = 0.995$ and $0.79 < \bar{U}_c < 1$, $S < 1$. This curve will be discussed later, in reference to the transition region between the low and high Re domains.

The results discussed above all dealt with the low Re range. For comparison, we now show the equivalent energy ratio for high Re, i.e., the domain relevant to larger larvae as well as adult anchovy (>15 mm long). The results presented

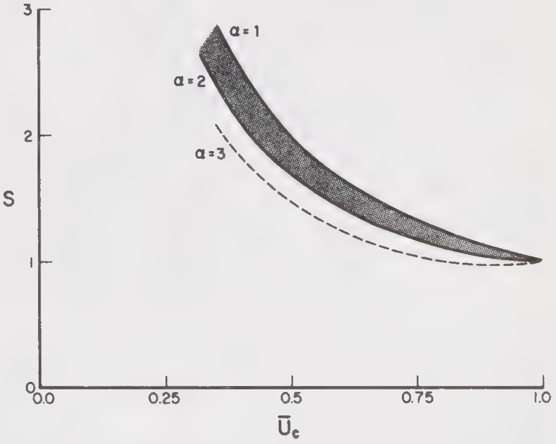

FIGURE 2.—Influence of changes in ratio of swimming drag to gliding drag α on the energy ratio S, versus nondimensional average speed $\bar{U}_c$. Shaded area is the range of possible α at low Reynolds numbers. $\bar{U}_f = 0.995$ (See Figure 1 for definitions).

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[2] Zweifel, J. R., and J. R. Hunter 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manuscr., 13 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

stem from calculations based on the analysis in Weihs (1974). The ratio of energy per unit distance traversed in intermittent swimming to that of continuous swimming at the same average speed R, can be shown to be, in present notation,

$$R = \frac{\tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i\bar{U}_f}\right)\left[\tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i\bar{U}_f}\right) + \alpha\left(\frac{1}{\bar{U}_i} - \frac{1}{\bar{U}_f}\right)\right]}{\left[\ln\left\{\cosh\left[\tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i\bar{U}_f}\right)\right] + \bar{U}_i \sinh \tanh^{-1}\left(\frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_i\bar{U}_f}\right)\right\} + \alpha \ln \frac{\bar{U}_f}{\bar{U}_i}\right]^2} \tag{25}$$

The computed values of R, for $\alpha = 2$, appear in Figure 3. Each full line describes the values of R for a given $\bar{U}_f$ as a function of the average velocity U_c. Each of these curves ends at $\bar{U}_c = \bar{U}_f$ and, in a similar manner to Figure 1, has a minimum for a lower value of U_c. Here, however, all curves have a large section in the range $R < 1$, i.e., intermittent swimming is more efficient. In fact, the slower the average velocity, the higher the possible gains, as shown by the dashed line which is the locus of lowest values of R as a function of $\bar{U}_c$. As already mentioned in Weihs (1974), this curve goes monotonously from unity at $\bar{U}_c = 1$ (continuous swimming by definition) to $1/\alpha$ at $U_c \rightarrow 0$. One can therefore predict that fish species using the anguilliform swimming mode (Breder 1926) will find intermittent swimming relatively more efficient than carangiform swimmers as α is greater for anguilliform swimming in which most of the body is oscillated. Another result is that for greatest gains, the average speed during the whole beat-and-glide should be as low as possible, with small differences between $\bar{U}_i$ and $\bar{U}_f$.

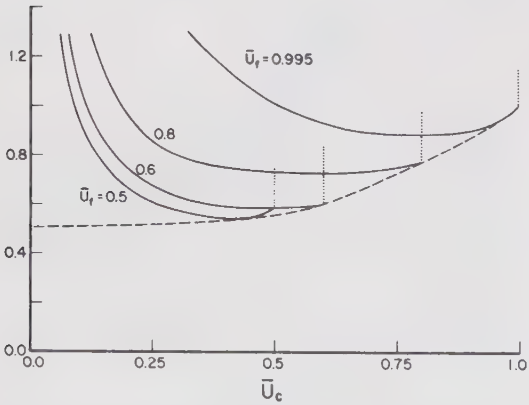

FIGURE 3.—The ratio of energy required per unit distance R, for intermittent and continuous swimming at high Reynolds numbers, respectively, versus nondimensional average speed U_c. Dashed lines shows locus of minimum values of R attainable as a function of $\bar{U}_c$. See Figure 1 for definitions.

Anchovy, which swim in the anguilliform mode, fulfill both these predictions as adults and more mature larvae usually swim by means of a single beat followed by a long glide, so that 1) $\bar{U}_i$ and $\bar{U}_f$ are not too different and 2) $\bar{U}_c$ is rather low.

Having examined the low and high Re domains, where the drag coefficient is porportional to the reciprocal of Re, and constant, respectively, we now look at the transition regime between them. Based on average swimming speeds of 0.8 body length/s, larvae will be in this regime when they are from 5 to 15 mm in length. Analysis of the forces and energy is much more complicated here because the hydrodynamic drag is

$$C_D \propto \mathrm{Re}^{-\beta} \tag{26}$$

where β is not constant, but itself is a function of both Re and body shape. This results in Equation (4) taking the form

$$T = m\frac{du}{dt} + \alpha K u^{2-\beta} \tag{27}$$

a differential equation that has to be solved numerically when β is not zero or one (the two cases discussed previously). While this in itself is a relatively straightforward task, the generality and accuracy of the previous solutions is immediately lost as numerical values for the mass and K have to be included. K especially is known very inaccurately as it includes the numerical drag coefficient and the frontal area (which varies at different speeds and times). The setting of β is even more problematical as it depends on the instantaneous swimming speed in an empirical manner (which is, however, not known at the present time), thus changing during the beat-and-glide cycle. No single value may therefore be taken to describe a given beat-and-glide behavior and an average value has to be used. This adds greatly to the inaccuracy as β is an exponent. Bearing especially the latter factor in mind, no smooth curves of the type appearing in Figures 1-3 can be expected.

In order to try and make clear how the transition regime influences the energetics of swimming, in spite of the difficulties mentioned, curves such as those from Figures 1 and 3 are reproduced in Figure 4. The purpose of this Figure is to show that by using the correct nondimensional description, curves for the viscous and nonviscous regimes can be compared. Both the dashed and full curves have similar shape, going to infinity for $\bar{U}_c \rightarrow 0$ and having a minimum at the higher values of $\bar{U}_c$, the values increasing again for $\bar{U}_c \rightarrow \bar{U}_f$. One must recall that the absolute speeds and sizes are very much different for the two cases, this resulting from the difference in U_0, the maximum sustained speed. U_0 is much larger for the full curves. The dashed curves have $\beta = 1$ while the full lines are for $\beta = 0$. Therefore, calculations at any intermediate values of β are expected to fall between them.

Some calculated values appear in Figure 4, for two values of average β. While they show the expected behavior, their actual values are, as mentioned before, unreliable, because they are based on rough estimates of various coefficients which do not have to be made when $\beta = 0$ or 1. These computations are to be taken only as an indication that the expected gradual transition actually occurs and are not to be used for actual calculations.

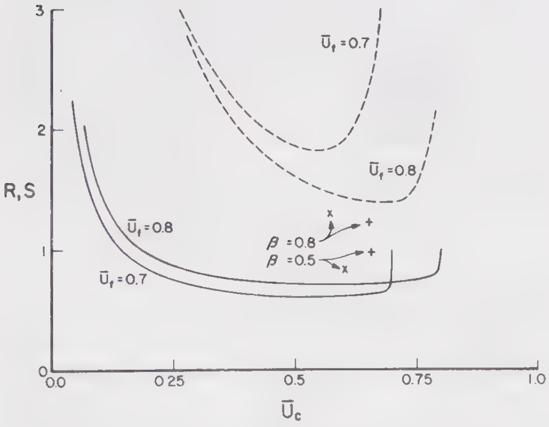

FIGURE 4.—Energy ratio versus nondimensional speed at various Reynolds numbers. Dashed lines show the low Reynolds number (viscous) regime, full lines are for high Reynolds numbers (boundary layers) and, ×, + are at intermediate Reynolds numbers, for $\bar{U}_f = 0.7$ and $\bar{U}_f = 0.8$, respectively. See Figures 1 and 3 for other definitions.

Keeping these limitations in mind, one can tentatively come to the conclusion that the intermediate Re regime is one of gradual transition. The advantage of beat-and-glide intermittent swimming becomes more and more significant as the larva grows, after the 4th day after hatching.

This conclusion can be strengthened, in a roundabout manner, by a different approach. The ratio of swimming to gliding drag for a given animal is 2 in the low Re regime, and up to 4 for high Re. Therefore taking a higher value of α for the viscous domain calculations can indicate, in a different manner, the trend of results when increasing Re. This appears in Figure 2, where the dashed line stands for $\alpha = 3$. It can be seen that this curve is intermediate between typical curves for the viscous (Figure 1) and inertial regimes (Figure 3).

CONCLUDING REMARKS

It was demonstrated in the previous section that the change in swimming style observed when anchovy larvae reach the age of 4-5 days is correlated with the passage of the animal from the highly viscous regime to the boundary layer regime. My calculations show that this behavioral change is an adaptive energy sparing mechanism. When the larva is <5 mm long, it can only progress by actively swimming as the enhanced effect of viscosity will bring it to a rapid halt when coasting. The yolk-sac, which still exists as a spherical protrusion, increases the drag even further at this stage. The drag coefficient here is inversely proportional to the velocity so that any low-speed motion is very costly in terms of energy. As a result, interspersing coasting and accelerating is not an efficient way of progressing. When the larva is larger (>5 mm) and moving faster, viscous effects are concentrated in a thin layer surrounding the fish and the influence of speed and shape on drag changes. At this stage, it is shown that intermittent motion is the more efficient for fish species such as anchovy which swim in the anguilliform mode. Intermittent motion is much less efficient for carangiform swimmers at all sizes (Weihs 1974) which may explain why species such as mackerel swim continuously at all phases of life.

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RESPIRATION AND DEPTH CONTROL AS POSSIBLE REASONS FOR SWIMMING OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, YOLK-SAC LARVAE

DANIEL WEIHS[1]

ABSTRACT

Larval northern anchovy in the yolk-sac (nonfeeding) stage exhibit regular bursts of continuous swimming during the first 3 days after hatching. It has been suggested that this behavior may have a respiratory function. A different possibility is depth control, countering the tendency of the larvae to sink when motionless. This paper includes a theoretical and experimental investigation of the possible functions of these swimming bouts.

The theoretical approach was to define a model and calculate the oxygen available to the larva when resting and while moving, and experiments were performed as a check of the theoretical results. The experiments were conducted on yolk-sac larvae in sealed tanks with varying dissolved oxygen concentrations to determine the effects of reducing the available oxygen on the frequency and duration of the swimming bursts. Results of the experiments confirmed the theoretical model. They indicate that the swimming bouts both help the larva stay at a constant depth and have a respiratory function when the oxygen concentration in seawater is less than 60% of saturation.

Newly hatched northern anchovy, *Engraulis mordax*, larvae exhibit a pattern of regular short bouts of continuous swimming interspersed with periods of resting. These larvae are still in the yolk-sac stage and are not feeding so that the locomotory behavior must have some other purpose, as these motions are energy consuming and also endanger the animal by attracting predators (Lillelund and Lasker 1971). Hunter (1972) suggested that these swimming bouts might have a respiratory function. Respiration has to be by cutaneous diffusion through the 2-3 μm thick skin (Lillelund and Lasker 1971) of the larvae as the gills develop only at a later stage. The purpose of this paper is to test this hypothesis and another possibility, depth control, to counter sinking due to the negative buoyancy, using theoretical and experimental methods.

First, I develop a theoretical model for oxygen transport to motionless and swimming yolk-sac larvae and estimate the possible oxygen uptake. Next, I describe the experiments to test the prediction of the theory for both proposed mechanisms and compare their results.

METHODS

Analytical Model

A mathematical model is now introduced to consider the possible respiratory function of the bouts of continuous swimming of yolk-sac anchovy larvae. First, we calculate the oxygen transport to a motionless larva. This transport is then compared with the metabolic requirements. If the metabolic requirements are not met, larval motion (and the resulting convective diffusion) is required.

The size of yolk-sac larvae (2.7-4.0 mm total length) and their swimming speeds (Hunter 1972) lead to typical Reynolds numbers, based on larval length (Weihs 1980) of <20. (The Reynolds number is a nondimensional factor indicating the relative importance of pressure and viscous effects on a body moving in a fluid under given circumstances—the higher the Reynolds number, the smaller the influence of the viscosity.) The larvae, as a direct result of their small size, are in a highly viscous laminar flow situation in which turbulent effects can be neglected. Thus, the larvae and their immediately surrounding water would be transported together in oceanic turbulent eddies, which are of the order of tens of centimeters in diameter. As a result, a nonswimming larva would stay for a relatively long period in the same mass

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of water, even though that mass is convected on a much larger scale.

The motionless larva and its surrounding water mass may therefore be analyzed separately, as a distinct system in the thermodynamic sense. Within this system, oxygen transport to the larva is controlled by molecular diffusion because the gill system is not developed at this stage. This process is time dependent, beginning when the larva arrives in a certain location (by swimming) and rests, ending when swimming begins again. Initially the oxygen concentration in the water mass surrounding the larva is uniform, but the larva now starts acting as an oxygen sink, gradually depleting the oxygen content of the water surrounding it. This concept of the larva as an oxygen sink simplifies the calculations, as knowledge of the exact distribution of oxygen diffusivity on the animal's surface is not required. The sink model also is useful here as it averages out the direction of local transport and the body of the larva into which the oxygen diffuses can be taken as an equivalent sphere of equal surface area (Figure 1).

Diffusion into a sphere is most conveniently analyzed in the spherical coordinate system. The governing conservation of mass equation can be written (Crank 1975) as

$$\frac{\partial c}{\partial t} = D\left(\frac{\partial^2 c}{\partial r^2} + \frac{2}{r}\frac{\partial c}{\partial r}\right) \tag{1}$$

where c is the mass fraction of oxygen (a function of the distance and time); r is the radial distance, measured for the center of the equivalent spherical body (the sink); t is the time; and D is the diffusion coefficient of oxygen in seawater.

The temporal boundary condition is the initial, uniform state

$$c(r,0) = c_0 \tag{2}$$

while the spatial conditions are

$$c(\infty, t) = c_0 \tag{3}$$

which states that far from the animal the oxygen concentration stays unchanged at all times. Strictly, the condition should be defined at some finite distance but as that distance is much larger than the animal equivalent radius, it can be approximated by ∞. Next, the oxygen concentration boundary condition at the surface of the equivalent sphere $r = a$ is obtained. Muscles and vascularized tissues have much higher oxygen transport rates than seawater, due to internal uptake augmented by active transport. Thus, oxygen will be absorbed at the surface of the larva as fast as it arrives by diffusion from the surrounding water. The oxygen concentration c at the larva's surface $(r = a)$ is thus constant, and very low, i.e.,

$$c\,(a,t) = c_1 \tag{4}$$

where $c_1 \to 0$ and $t>0$.

Equations (2)-(4) enable solving equation (1) analytically, by classical methods. The solution can be written in nondimensional form for the concentration as

$$\frac{c - c_0}{c_1 - c_0} = \frac{a}{r}\,\mathrm{erfc}\,\frac{r-a}{2\sqrt{Dt}} \tag{5}$$

where the complementary error function, erfc, is defined as

$$\mathrm{erfc}(z) = \frac{2}{\sqrt{\pi}}\int_z^{\infty} e^{-z^2}\,dz\,. \tag{6}$$

Numerical values of the complementary error function are found in most mathematical tables (e.g., Abramowitz and Stegun 1965).

The rate of mass transfer (flux) J to the animal is now obtained from

$$J = -\rho D \int_A \frac{\partial c}{\partial r}\,dA \quad \text{(surface A)} \tag{7}$$

where ρ is the density and A the surface area of the body. For the equivalent sphere of radius a, $A = 4\pi a^2$. $\partial c/\partial r$ is assumed spherically symmetric so that

$$J = -\rho D A \left.\frac{\partial c}{\partial r}\right|_{r=a} \tag{8}$$

where the concentration derivative is obtained from Equation (5). Substituting this, and the value for the surface area, and setting $c_1 = 0$ as in Equation (4), the total mass flux per unit time J_d is

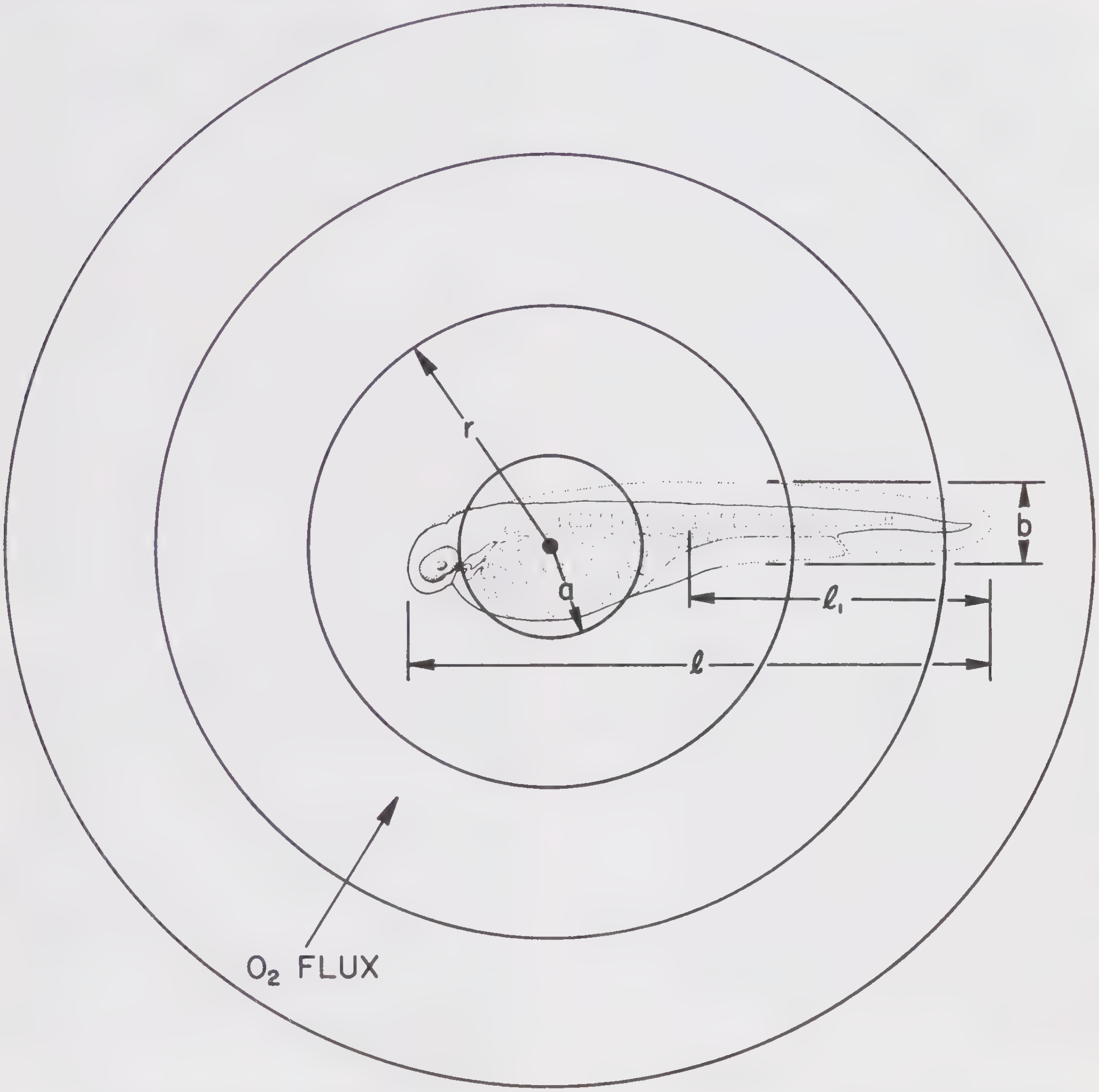

FIGURE 1.—Schematic description of model and spherical coordinate system centered on the center of mass of a northern anchovy larva: a is the radius of an equivalent sphere of equal surface area (not to scale), l is the larval length, and b and l_1 are the average tail strip depth and length.

$$J_d = -\rho D c_0 \cdot 4\pi r^2 \frac{a}{r} \operatorname{erfc}\left(\frac{r-a}{2\sqrt{Dt}}\right) \cdot \left(\frac{1}{2\sqrt{Dt}} + \frac{1}{r}\right) \qquad (9)$$

and when $r = a$, this simplifies to

$$J_d = 4\pi\rho D c_0 a^2 \left(\frac{1}{a} + \frac{1}{2\sqrt{Dt}}\right) \qquad (10)$$

Equation (10) consists of two terms in the brackets, multiplied by a constant factor. The first term in the brackets is the constant, time-independent contribution while the second describes the initial transient. The latter drops rapidly, proportionally to the square root of time elapsed since arrival of the larva. Substituting numerical values into Equation (10), the oxygen flux can be compared with oxygen requirements of larval anchovy to see if the swimming motions are required for respiration.

The equivalent radius, a, of the larval anchovy is found by equating the surface area of the larva and the equivalent sphere. The larva, at this yolk-sac stage, is described for diffusion purposes as a sphere of radius q (the yolk sac) attached to an almost flat ribbon of length l_1 and average breadth b. The combined surface area of the sphere and ribbon is then taken to be equal to the area of the equivalent sphere appearing in Equation (10). Thus

$$4\pi a^2 = 2\, l_1\, b + 4\pi q^2. \qquad (11)$$

Using typical values for these parameters for newly hatched larvae we obtain $l_1 = 1.4$ mm, $b = 0.3$ mm, and $q = 0.3$ mm (from drawings by E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038), i.e., $a = 0.0395$ cm. The mass content of oxygen in seawater at 20° C is $c_0 = 7.8 \times 10^{-6}$ g/cm^3 (Prosser 1973), and the mass fraction is obtained by dividing by the density of seawater, which then cancels out in Equation (10). Finally, the diffusion coefficient of oxygen is approximately equal for freshwater and seawater (Riley and Skirrow 1965) so that a reasonable value for 20° C is 1.8×10^{-5} cm^2/s (O'Brien et al. 1978), or $D = 1.08 \times 10^{-3}$ cm^2/min. Substituting all these values into Equation (10) we obtain

$$J = (4.18 + 2.51\, t^{-1/2})\, 10^{-9} \text{ g/min} \qquad (12)$$

when the water is 100% saturated. Reducing the oxygen content of the water causes the value of the oxygen flux, J, to go down proportionally, i.e., by multiplying J from Equation (12) by the fraction of saturation. Some typical values of J appear in Figure 2 with the percent of saturation as the parameter.

When the larva starts swimming, two changes in the oxygen supply occur. First, the animal's motion produces a convective local flow relative to the body, thus bringing new, oxygen-rich water closer and removing the respiratory waste products. Secondly, the absolute motion will bring the larva to an area where the oxygen concentration is still at the initial ambient value, starting the process described by Equations (1)-(4) again.

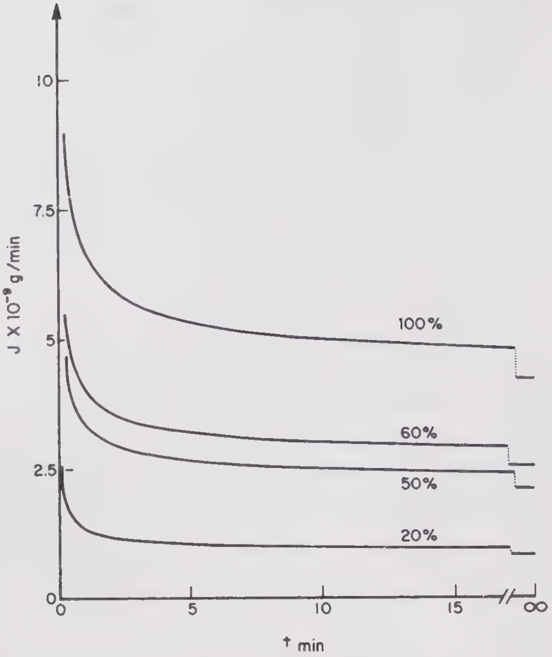

FIGURE 2.—Rate of oxygen transport (J) to motionless northern anchovy larva by diffusion versus time (t). Broken part of curve shows asymptotic value, after the initial transient has disappeared. Parameter is oxygen concentration in percentage of saturation.

Following this reasoning, even relatively slight motions causing just a local flow around the animal's body would suffice for respiratory functions. Thus, actual swimming would not be required. However, the yolk-sac larvae are increasingly negatively buoyant with age (Hunter and Sanchez 1976), which causes them to sink. Therefore, active absolute motion is necessary for the larva to stay at a given depth for feeding and future schooling.

When the larva is swimming, the process of transport of oxygen changes to convective diffusion, and as such is described by a different model (Daykin 1965). Daykin's work dealt with stationary eggs in a moving river environment, but for mass transfer purposes this is equivalent to a larva (or egg) moving at constant speed relative to the water. In the convective diffusion process (Levich 1962; Daykin 1965), the mass transfer to the larva can be roughly described by

$$J_{\text{con}} = 4\pi a^2 (c_0 - c_1) k \qquad (13)$$

where k is a diffusion coefficient obtained from experimental correlations of the diffusional flux with the Reynolds (Re) and Schmidt numbers (Sc). (The Schmidt number is the ratio of the kinematic viscosity to the diffusivity and nondimensionally indicates the relative importance of these two effects in a given flow situation.) For the present circumstances

$$k = \frac{D}{2a}\left(2 + 0.6\ \mathrm{Re}^{1/2}\ \mathrm{Sc}^{1/3}\right) \qquad (14)$$

for average swimming speeds of approximately 5 cm/s (Hunter 1972) and a Schmidt number of 600 we have

$$J_{\mathrm{con}} = 1.27 \times 10^{-7}\ \mathrm{g/min}. \qquad (15)$$

Hence, oxygen transport due to convective diffusion is over 20 times higher than for the motionless larva (Equation (12)). The calculation leading to Equation (15) is approximate, as the larva's shape will influence the coefficient 0.6 in k (Equation (14)) and also change the form of Equation (13). It is, however, accurate to at least an order of magnitude (Levich 1962). Thus, once the larva starts swimming, the mass transfer of oxygen to its surface increases by at least an order of magnitude. Recently, an additional mechanism for oxygen transport to stationary eggs was identified by O'Brien et al. (1978) who showed that under certain riverbed conditions natural convection, due to the oxygen and metabolite gradients, may contribute to the oxygen transfer. This effect may play a supplementary role in the present (pelagic) case as the natural convection effects are much smaller than the forced convection.

Tests with Larvae

Egg batches were obtained once a week from groups of adult northern anchovy maintained in the laboratory and induced to spawn. Measurements were made each week during a 6-wk period to minimize bias due to a single cohort group. Water temperature ranged from 19° to 21° C, and overhead fluorescent lighting was used. The 50% hatching point was determined and defined as "day 0" for each batch. Experiments were carried out on age day 0 larvae every week (six times).

A set of five 2,000 ml graduated cylinders filled with filtered seawater was used for the environmental tests. Oxygen concentrations of 100, 80, 60, 40, and 20% of saturation at the measured temperature were produced by bubbling nitrogen through each of the cylinders. After the larvae were added (about 25 individuals/cylinder), the cylinders were sealed off with rubber stoppers. Oxygen concentrations were measured periodically during the experiments with a Beckman Instrument Model 160 Physiological Gas Analyzer[2] to check on initial values and possible drift.

Individual fish were monitored for a 5-min period, and duration and number of swimming bursts were recorded on a Esterline-Angus Operation Recorder Model AW. Records were also made of approximate swimming direction (measured from horizontal) as well as the change in orientation of motionless larvae while they were sinking during the resting periods. Five active larvae were monitored in each container every week, for both day 0 and day 1 tests.

After the day 0 experiments were finished each week, the equipment was reset and the day 1 tests conducted 24 h later with additional larvae from the same batch. The latter larvae were kept in oxygen-saturated water from hatching to minimize stress due to oxygen starvation.

RESULTS

No appreciable change in the proportion of time spent in burst swimming was observed when the measurement at 100% of saturation concentration of oxygen (which is the oxygen level in the natural state in the sea because of turbulent interchange with the atmosphere) was compared with the time spent in motion at the 80 and 60% oxygen levels (Figure 3).

When oxygen levels were <60% of saturation, large increases in the time spent swimming were observed. The rate of increase of swimming time in both ages (day 0 and day 1) were similar. Various attempts at describing all five data points for each age-group by means of a single empirical exponential function were not successful (low coefficients of determination). Thus, it seems that a different behavioral mechanism is triggered when oxygen levels fall below 60% of saturation at the given temperatures, i.e., much lower than expected oxygen concentrations in the upper layers of the sea, where the anchovy larvae are usually found.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

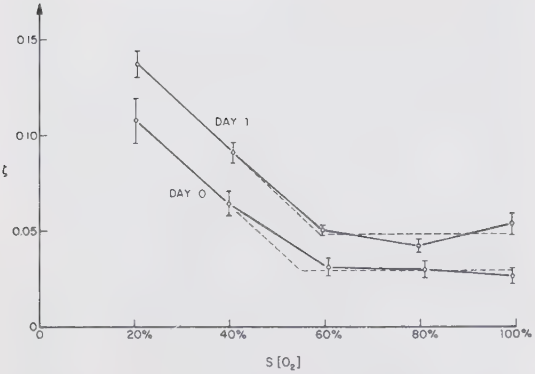

FIGURE 3.—Fraction of time spent actively swimming, ζ, versus oxygen concentration in percentage of saturation. $S[O_2]$, for newly hatched (day 0) and 24-h-old (day 1) northern anchovy larvae. Each point on the full curves is an average of between 20 and 25 individual 5-min observations. Bounds are standard errors. Dashed lines indicate idealized model of constant fraction, ζ, at high $S[O_2]$ and linearly increasing ζ at low $S[O_2]$.

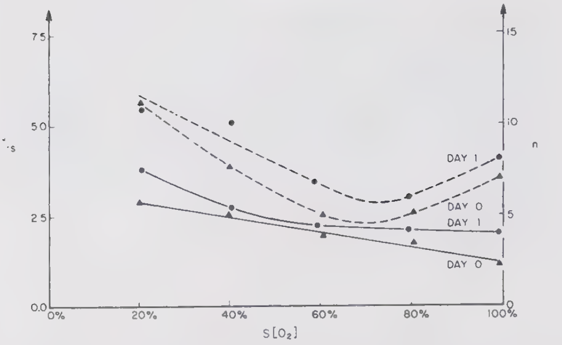

FIGURE 4.—Average duration (t) of swimming bouts (full lines) and number of bouts (n) in 5 min (dashed lines) for day 0 (solid triangles) and day 1 (solid circles) larvae, versus oxygen in percentage of saturation concentration ($S[O_2]$).

The duration of bursts increased monotonically as the oxygen levels decreased, while the number of bursts dropped significantly to a minimum of 1/min at 60-80%, increasing sharply after that (Figure 4). No satisfactory explanation has been found for the drop in the number of bursts at 80% of saturation. The main result illustrated by Figure 4 is that both the frequency and duration of bursts increase markedly at low oxygen concentrations, both contributing to the increase in time spent swimming.

The center of gravity of anchovy larvae is in the vicinity of the head and therefore they tend to be oriented in an oblique head-down configuration after swimming ceases. More mature larvae, which have converted significant amounts of yolk into denser tissue are negatively buoyant (Hunter and Sanchez 1976) and tend to sink head downward at rates of approximately 1-2 mm/s. To check the vertical station-keeping hypothesis, the direction of swimming was recorded, as well as the body orientation, when swimming started. The results of over 1,400 recorded swimming periods appear in Table 1, which lists average values of the body angle at the onset of swimming and the direction of swimming.

No significant variation in swimming direction with oxygen concentration was found for either day 0 or day 1 larvae (Table 1). The spread in results was large, as is noticeable from the standard errors. The total possible spread of data is ±90°, which suggests that swimming direction is actually a random phenomenon for day 0 larvae. At age 1 day, a positive bias was observed in the swimming direction, still with large variation. The body inclination at the beginning of the swimming periods was consistent, at around −65° with the exception of the day 0, 20% oxygen data, which is influenced by additional factors, discussed below.

DISCUSSION

The analytical model predicted that a motionless larva would be able to pick up oxygen at a decreasing rate at any given spot (Equation 12).

TABLE 1.—Initial orientation of the body and duration of swimming during bouts of continuous swimming by newly hatched and 1-d-old northern anchovy larvae. Error bounds are standard error. Angles are measured from the horizontal. Positive values indicate upward motion. Averages of day 0 do not include 20% O_2 values as these (indicated by question marks) include different phenomena.

Oxygen concentration (% of saturation)	*N*, number of observed events		Orientation of body at start of swimming period (degrees)		Direction of swimming relative to horizontal (degrees)	
	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae
100	106	157	−68.9±23.7	−74.6±11.8	−4.7±56.1	44.7±45.8
80	103	113	−66.3±29.4	−80.0± 9.2	−15.0±59.0	28.2±58.1
60	109	112	−72.1±15.6	−66.7±17.6	−3.9±73.6	51.9±31.9
40	161	140	−61.0±30.3	−69.2±22.0	12.3±54.0	33.2±45.9
20	210	204	−45.6±36.7(?)	−63.8±27.8	38.7±43.3(?)	37.4±52.3
Weighted average			−66.4±25.2	−70.2±16.9	−2.8±58.3	39.0±48.1

This prediction has now to be compared with the requirements of the organisms to determine if additional oxygen is needed. Data for oxygen consumption at 17° C of late-stage anchovy eggs and larvae of differing ages as a function of time since spawning has been obtained by Theilacker,[3] by measurement in a respirometer. These data were adjusted to 20° C, the temperature at which most of my experiments were conducted (Figure 5), by means of a temperature-growth correlation for larval northern anchovy (Zweifel and Hunter[4]). This adjustment was made by calculating the size of the larvae at 17° C at the ages recorded by Theilacker, then translating these into age for the same size at the new temperature, which gave a smaller size because growth rates increase with temperature. Thus, an estimate for the oxygen requirements at 20° C of size-defined larvae was obtained as a function of their age (the 20° C line in Figure 5).

The value of the ratio of oxygen consumption 1 d after hatching to that at hatching was about 1.6 (Figure 5). Returning now to Figure 3 we see that the ratio for the average percent of time spent swimming of the two age-groups is approximately 1.66. I conclude, therefore, that the distance between the day 0 and day 1 curves in Figure 3 is an indication of the increased general activity of the larvae as they grow. This correlation indicated in Figures 3 and 5 serves as an additional verification of both Theilacker's respirometer data and the present swimming data.

To compare experimental values of oxygen consumption to the prediction of the model we plot the data as Figure 6, where the horizontal lines show the range of oxygen requirements (from Theilacker's data) at hatching and 24 h later. The steady-state oxygen available by steady-state diffusion only (after the initial transient) obtained from the time-dependent first term in Equation (12) is now superimposed. Figure 6 indicates that pure diffusion supplies all the oxygen required for the day 0 larvae only when $<42 \pm 4\%$ of the O_2 saturation concentration is available. This changes to $63 \pm 4\%$ of saturation for the day 1 larvae. The sharp discontinuity in the swimming data, occurring be-

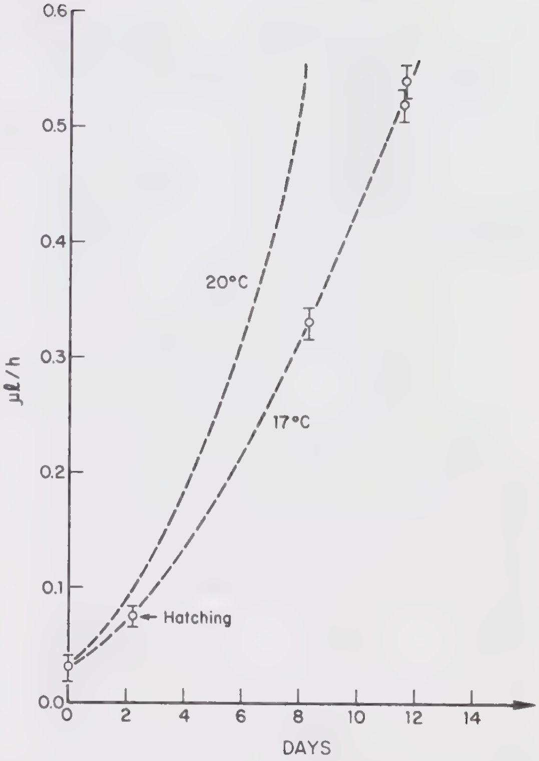

FIGURE 5.—Oxygen consumption by northern anchovy eggs and larvae versus time elapsed since spawning. Open circles indicate experimental data for 17° C. The line for 20° C is extrapolated from the 17° C data with the aid of the Zweifel and Hunter model (see text).

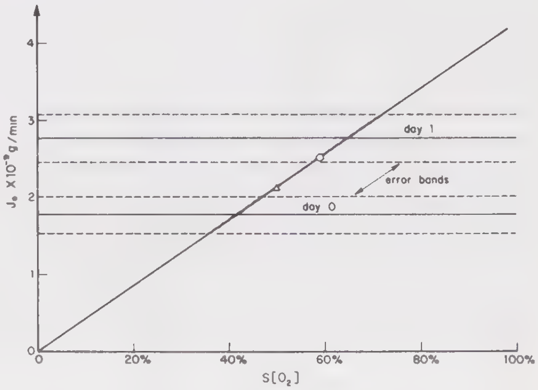

FIGURE 6.—Estimated oxygen requirements (J_0) of northern anchovy larvae at day 0 (hatching) and day 1, and steady-state oxygen supply by diffusion versus oxygen in percentage of saturation concentration ($S[O_2]$). The triangle and circle denote concentrations at which observed swimming behavior changes at day 0 and day 1, respectively (see Figure 3).

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[3] G. Theilacker, Fishery Biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92030, pers. commun. November 1978.

[4] Zweifel, J. R., and J. R. Hunter. 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manuscr., 37 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

tween 60 and 40% oxygen concentration (Figure 3) can now be understood in terms of the theoretical results above. When the oxygen concentration in this water is 60% or higher, diffusion alone can satisfy the respiratory requirements of both day 0 and day 1 motionless larvae. Thus, the swimming activity at the higher concentrations is due to other factors, such as depth control. The measured activity level (Figure 3) does not change between 60 and 100% oxygen concentration, as expected from the theoretical model's predictions.

The increased swimming activity observed when the concentration drops below the 40-60% level must therefore be a respiratory reaction. Active swimming causes convective diffusion (which, as shown in the Analytical Model section, leads to much higher oxygen transport rates) and moves the larva to a new, nondepleted position. As expected from this mechanism, activity increases with decreasing ambient oxygen concentration, as oxygen transport rates drop below the required level faster at low ambient concentration, initiating motion more often. The dashed lines in Figure 3 verify this theoretical reasoning and the obtained values of 59% concentration (day 1) and 55% concentration (day 0) for the beginning of respiration-driven swimming are in very good agreement with Figure 6, especially considering the experimental errors involved in the various data sources.

Next, I consider the significance of swimming activity at higher oxygen concentration. The most plausible reason for the swimming behavior is to keep the larvae, which are negatively buoyant, from sinking out of the preferred depth zone in the sea. Day 1 larvae swim at an average angle of 39° upwards from the horizontal with no significant variation with oxygen concentration (Table 1). The large standard error is an indication of the wide spread of observed directions. The average swimming speed at this stage is 5.2±4.1 cm/s (Hunter 1972) and the average duration of a swimming bout (at oxygen concentration of 60-100%) is about 2.1 s (Figure 4). The average vertical component of the distance moved during a single bout is therefore

$$h_{\mathrm{up}} = Vt \sin \alpha = 5.2 \cdot 2.1 \sin 39^\circ = 6.9 \text{ cm}. \quad (16)$$

The uncertainty in this value is large due to the standard errors in both the swimming angle and the average swimming speed, but it is probably accurate at least to an order of magnitude. Between swimming periods, the larvae sink at a speed of 0.12±0.03 cm/s (Hunter and Sanchez 1976). The average number of swimming bouts per 5-min period was found to be about 7 (Figure 4), i.e., giving an average sinking time of 43 s. This leads to a vertical distance of 5.2 cm, which is close enough to the value of 6.9 cm of Equation (16) to show that the swimming of day 1 larvae at high oxygen levels most probably is a depth-control mechanism.

The newly hatched (day 0) larvae present a different situation. Pelagic eggs are slightly positively buoyant (Blaxter 1969) while the chorion, which is shed during hatching, is somewhat negatively buoyant. Thus, while no measurements independent of the present ones exist, it is reasonable to assume that these newly hatched larva are approximately neutrally buoyant due to their large yolk sac. As the yolk is consumed, the specific gravity increases and the sinking rates for day 1 are obtained. The larvae are approximately neutrally buoyant during the first hours after hatching so that no net sinking or upward swimming is expected. Table 1 shows that this is actually the case at day 0, where the average direction is very close to horizontal and the large error indicates almost random swimming direction. Some upward swimming may be discerned at the very low O_2 concentration experiments (20% O_2). This may be a result of an inadvertent oxygen gradient in the tank or a phototactic response induced by the low oxygen concentration. Phototaxis is probably the means by which the older larvae choose swimming direction, and is directed upwards as light in the present experiments comes from the surface.

ACKNOWLEDGMENTS

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Synopsis of Biological Data on Bonitos of the Genus *Sarda*

HOWARD O. YOSHIDA[1]

ABSTRACT

Published and some unpublished information on the biology and resources of the three species of *Sarda, S. australis, S. chiliensis,* and *S. sarda,* are compiled, reviewed, and analyzed in the FAO species synopsis style.

INTRODUCTION

In response to a growing demand for tuna, increased effort has been expended over the years to harvest the commercially important large tunas throughout the world's oceans. The effort has increased to such an extent that some of the tunas are in danger of being overexploited. Examples of these are the yellowfin tuna, *Thunnus albacares,* in the eastern tropical Pacific, which has been under management now for a number of years, and the albacore, *T. alalunga,* of the South Pacific Ocean (Skillman 1975). To meet the demand for tuna and at the same time avoid the overexploitation of important resources, attention has been focused on tuna resources that are relatively underutilized, such as the skipjack tuna, *Katsuwonus pelamis.* In addition, some of the smaller tunas or tunalike species such as the bonitos, *Sarda* spp., which up to now have had mixed acceptance in the marketplace, are gaining more attention.

The bonitos are not an entirely unutilized resource. The total world catch of bonitos has ranged from about 92,200 to 140,500 t (metric tons) in the 10-yr period from 1964 to 1973 (Food and Agriculture Organization of the United Nations 1970, 1974). As indicated above, however, bonitos have varying acceptance throughout the world. In the Mediterranean and Black Sea countries, *Sarda sarda* is of great importance and has been the object of a fishery for many years (Demir 1963). In Chile, in contrast to earlier years when *S. chiliensis* contributed insignificant amounts to the total fish processed, more and more bonitos have been processed into canned products in recent years (Barrett 1971). In California waters, *S. c. lineolata* has been exploited since the beginning of the century and there are indications that the California Indians utilized this species before the arrival of Europeans (Klawe[2]). It does not have much commercial value, however, and the California tuna industry has accepted bonito more from necessity than by choice (Frey 1971). The flesh of *S. orientalis* is considered rather soft and inferior in quality, and except in Kyushu, where it is caught as an adjunct to the mackerel and other pelagic species, bonitos are not especially sought after in Japan (Kikawa and Staff of the Nankai Fisheries Research Laboratory, Kochi, Japan 1963). And in Australia, the edible qualities of *S. australis* are not highly regarded (Grant 1972).

The purpose of this report is to review and analyze all the information available on the biology and resources of the bonitos throughout the world, following the FAO (Food and Agriculture Organization of the United Nations) species synopsis style (Rosa 1965). This report is based on published papers, in general, and the FAO species synopses on the bonitos (Demir 1963; Kikawa and Staff of the Nankai Fisheries Research Laboratory, Kochi, Japan 1963; Idyll and de Sylva 1963; Silas 1963) were heavily relied on. Ancieta (1964) also prepared a species synopsis on *S. chiliensis* in Peruvian waters in the FAO species synopsis style.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

The confusion on the number of valid species in the genus *Sarda* has been cleared and, basically, four allopatric species are now recognized (Collette and Chao 1975). These are the southeast Australian *Sarda australis* (Macleay 1880), the eastern temperate Pacific *Sarda chiliensis* (Cuvier 1831), the tropical Indo-Pacific *Sarda orientalis* (Temminck and Schlegel 1844), and the Atlantic *Sarda sarda* (Bloch 1793) (Fig. 1).

The Australian bonito was originally described as *Pelamys australis* Macleay 1880. Type-locality: Port Jackson, Sydney, Australia. Holotype: Macleay Museum, University of Sydney F-333, now at Australian Museum, Sydney.

The eastern temperate Pacific *Sarda chiliensis* was

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2] W. L. Klawe, Inter-American Tropical Tuna Commission, La Jolla, CA 92037, pers. commun. February 1978.

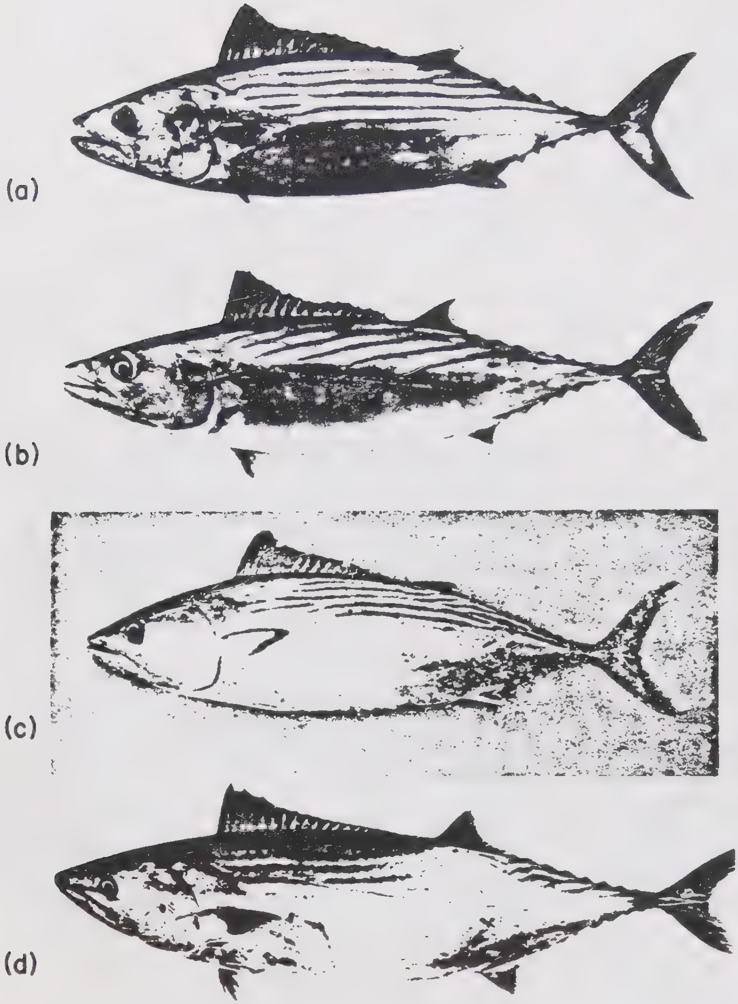

Figure 1.—The four species of *Sarda*: (a) *Sarda australis* (from Serventy 1941a, plate 4); (b) *Sarda chiliensis* (from Frey 1971); (c) *Sarda orientalis* (from Kikawa and Staff of the Nankai Regional Fisheries Research Laboratory 1963, fig. 1); (d) *Sarda sarda* (from Demir 1963, fig. 1a).

first described as *Pelamys chiliensis* Cuvier 1831. Type-locality: Valparaiso, Chile. Holotype: Muséum National d'Histoire Naturelle, Paris A.5608.

The tropical Indo-Pacific bonito was first described as *Pelamys orientalis* Temminck and Schlegel 1844. Type-locality: Japan. Three syntypes are in the Rijksmuseum van Natuurlijke Historie, Leiden, of which Boeseman (1947, 1964) selected the largest as lectotype, RMNH 2286.

The Atlantic bonito *Sardo sarda* was first described as *Scomber sarda* Bloch 1793. No types known to be extant.

1.12 Synonymy

The synonymies given below are modified versions of those given by Collette and Chao (1975) and do not distinguish objective and subjective synonyms.

Sarda australis (Macleay)

Pelamys australis Macleay 1880 (Port Jackson, Sydney, Australia)

Pelamys schlegeli McCoy 1888 (Prince Phillip Bay, Victoria, Australia)

Pelamys chilensis (not of Cuvier 1831) Ogilby 1893 (New South Wales, Australia)

Sarda chilensis (not of Cuvier 1831). Waite 1904 (New South Wales, Australia)

Sarda chiliensis (not of Cuvier 1831). McCulloch 1922 (New South Wales, Australia)

Sarda orientalis (not of Temminck and Schlegel 1844). Lord 1927 (Tasmania, Australia)

Sarda australis. Walford 1936

Sarda chiliensis australis. Roughley 1951 (Queensland, New South Wales, and Victoria, Australia)

Sarda chilensis australis. Silas 1964 (eastern Australia)

Sarda chiliensis (Cuvier)

Following Collette and Chao (1975) the synonymy for *S. chiliensis* is split for the southeast Pacific *S. chiliensis chiliensis* and the northeast Pacific *S. chiliensis lineolata* (see section 1.23 Subspecies).

Sarda chiliensis chiliensis (Cuvier)

Pelamys chiliensis Cuvier *in* Cuvier and Valenciennes 1831 (Valparaiso, Chile)
Pelamys chilensis. Günther 1860
Sarda chilensis. Starks 1906 (Callao, Peru)
Sarda chiliensis. Walford 1936
Sarda sarda chiliensis. Buen 1958 (Chile)
Sarda chilensis chilensis. Vildoso 1963 (Peru)
Sarda sarda chilensis. Sánchez and Lam 1970 (Peru)
Sarda chiliensis chiliensis. Kuo 1970 (Peru)

Sarda chiliensis lineolata (Gerard)

Pelamys lineolata Girard 1859 (San Diego, Calif.)
Pelamys chilensis. Günther 1860
Sarda chilensis. Jordan and Gilbert 1882
Sarda lineolata. Walford 1936
Sarda stockii David 1943 (Santa Monica Mountains, Calif.)
Sarda chiliensis. Chabanaud 1944
Sarda chiliensis lineolata. Kuo 1970 (Calif.)

Sarda orientalis (Temminck and Schlegel)

Indo-West Pacific

Pelamys orientalis Temminck and Schlegel 1844 (Japan)
Pelamys chilensis (not of Cuvier 1831), Day 1878
Sarda chilensis var. *orientalis.* Steindachner and Döderlein 1884 (Japan)
Sarda orientalis. Jordan and Snyder 1900 (Tokyo)
Sarda chilensis (not of Cuvier 1831), Jordan and Snyder 1904 (Honolulu)
Sarda chiliensis (not of Cuvier 1831), Fowler 1938 (Honolulu)
Sarda orientalis serventyi Whitley 1945 (Western Australia)

Eastern Pacific

Sarda chilensis (not of Cuvier 1831), Gilbert and Starks 1904 (Panama City)
Sarda chiliensis (not of Cuvier 1831), Herre 1936 (Galápagos)
Sarda velox Meek and Hildebrand 1923 (Panama City)
Sarda orientalis. Fraser-Brunner 1950

Sarda sarda (Bloch)

Scomber sarda Bloch 1793 (Europe)
Scomber mediterraneus Bloch and Schneider 1801
Scomber palamitus Rafinesque 1810 (Palermo, Sicily)
Scomber ponticus Pallas 1811 (Crimea)
Thynnus pelamis. Risso 1826 (Nice)
Thynnus sardus. Risso 1826 (Nice)
Thynnus brachypterus Cuvier 1829
Sarda sarda. Cuvier 1829
Pelamys sarda. Cuvier *in* Cuvier and Valenciennes 1831 (Cape Verde Islands and Brazil)
Palamita sarda. Bonaparte 1831
Pelamis sarda. Valenciennes 1844 (Canary Islands)
Sarda pelamys. Gill 1862
Sarda mediterranea. Jordan and Gilbert 1882 (both sides of Atlantic)
Sarda pelamis. Smitt 1892 (Scandinavia)

1.2 Taxonomy

1.21 Affinities

Suprageneric

- Phylum Chordata
  - Subphylum Vertebrata
    - Superclass Gnathostomata
      - Class Osteichthyes
        - Subclass Actinopterygii
          - Order Perciformes
            - Suborder Scombroidei
              - Family Scombridae
                - Subfamily Scombrinae
                  - Tribe Sardini

Generic

Genus *Sarda* Cuvier 1829.

The generic concept of Collette and Chao (1975) is followed.
Sarda Cuvier 1829:199 (type-species *Scomber sarda* Bloch 1793 by monotypy).
Pelamys Cuvier *in* Cuvier and Valenciennes 1831:149 (type-species *Scomber sarda* Bloch 1793 by original designation).
Palamita Bonaparte 1831:173 (substitute name for *Pelamys* Cuvier 1831 preoccupied by *Pelamys* Oken 1816 in Reptilia, Hydrophiidae; therefore, takes the same type-species *Scomber sarda* Bloch 1793).
Creotroctes Gistel 1848, p. X (type-species *Scomber sarda* Bloch 1793; substitute name for *Sarda* Cuvier 1829).

The species of *Sarda* all have several stripes dorsally, ranging from horizontal to oblique in orientation. The intestine runs straight from the stomach to the anus and there are two intermuscular bones on each side of the back of the skull. The bony caudal peduncle keels are well developed as in higher tunas, but are divided into anterior and posterior sections on each vertebra; the spleen is large and prominent in ventral view; the right and left lobes of the liver are both much longer than the middle lobe. The body is fusiform instead of being more laterally compressed. Collette and Chao (1975) compared the similarities and differences of the genus *Sarda* with the other genera of bonitos within the tribe Sardini.

Collette and Chao (1975) recognized four allopatric species of *Sarda: S. australis, S. chiliensis, S. orientalis,* and *S. sarda.*

Specific

A summary of characters distinguishing the four species of *Sarda* is given in Table 1.

A key to the species of *Sarda* as adapted from that given for the Sardini by Collette and Chao (1975) is presented below.

Key to the species of *Sarda*

1a Spines in first dorsal fin 20-23; total vertebrae 50-55 . . . . *S. sarda* (Bloch)
1b Spines in first dorsal fin 17-19; total vertebrae 43-46 2

2a Total gill rakers on first arch 8-13; supramaxilla narrow . . *S. orientalis* (Temminck and Schlegel)
2b Total gill rakers on first arch 19-27; supramaxilla wider 3

3a Total gill rakers on first arch 19-21; pectoral rays 25-27, modally 26; teeth sometimes present on vomer; length of first dorsal base 315-343 thousandths of fork length; maxilla 503-539 thousandths of head length . . . . *S. australis* (Macleay)
3b Total gill rakers on first arch 23-27; pectoral rays 22-26, modally 24 or 25; teeth never present on vomer; length of first dorsal base 267-314 thousandths of fork length; maxilla 460-503 thousandths of head length . . . . *S. chiliensis* (Cuvier)

1.22 Taxonomic status

As already noted four allopatric species of *Sarda* are recognized (Collette and Chao 1975).

1.23 Subspecies

Two subspecies of the eastern temperate Pacific *Sarda*

Table 1.—Summary of characters showing differences and similarities among the four species of *Sarda*. (From Collette and Chao 1975, table 17.)

Character (reference)	*S. sarda*	*S. australis*	*S. chiliensis*	*S. orientalis*
Lamellae in nasal rosettes	22-33 ($\bar{x}$ 26.5)	34-39 ($\bar{x}$ 37.2)	21-30 ($\bar{x}$ 25.4)	25-36 ($\bar{x}$ 31.9)
Vomerine teeth present	sometimes	sometimes	never	never
Upper jaw teeth	16-26	16-26	18-30 ($\bar{x}$ 23.5)	12-20 ($\bar{x}$ 15.5)
Lower jaw teeth	12-24 ($\bar{x}$ 16.0)	11-20 ($\bar{x}$ 14.5)	4-25 ($\bar{x}$ 19.2)	10-17 ($\bar{x}$ 13.0)
Palatine teeth	8-21 ($\bar{x}$ 12.3)	7-14 ($\bar{x}$ 10.7)	9-22 ($\bar{x}$ 15.2)	8-19 ($\bar{x}$ 11.9)
Supramaxilla width	intermediate	intermediate	wide	narrow
Ectopterygoid-dorsal portion	pointed	pointed	pointed	slightly expanded
Hyomandibular spine-condyle	projects beyond condyle	short	short	projects beyond condyle
Angle of hyomandibular spine	about 90°	about 90°	greater than 90°	less than 90°
Elliptical ceratohyal window	present	present	present	only slight depression
Ventral surface of glossohyal	depression present	depression present	depression present	no depression
Gill rakers	16-23	19-21	23-27	8-13
Vertebrae	50-55	43-46	43-46	43-46
Pleural ribs	24	19-23	19-23	19-23
Intermuscular bones	31-45	32-36	32-36	32-36
Keels on vertebrae number	5-10	5-8	5-8	5-8
First closed haemal arch	13th-15th vertebra	13th-15th vertebra	12th-14th vertebra	12th-14th vertebra
Length of haemal prezygapophyses and postzygapophyses at precaudal-caudal junction	postzygapophyses longer than prezygapophyses	postzygapophyses longer than prezygapophyses	prezygapophyses longer than postzygapophyses	prezygapophyses longer than postzygapophyses
Dorsal spines	20-23	17-19	17-19	17-19
Dorsal finlets	modally 8	modally 7	modally 8	modally 8
Anal rays	14-17 (modally 15)	14-17 (modally 15)	12-15 (modally 14)	14-16 (modally 15)
Anal finlets	modally 7	modally 6	modally 7	modally 6
Total anal elements	19-23 (modally 21-22)	19-23 (modally 21-22)	18-22 (modally 20)	20-22 (modally 21)
Supracleithral notch	wide angle	almost 90°	wide angle	wide angle
Pectoral rays	23-26	25-27 (modally 26)	22-26 (modally 24-25)	22-26 (modally 24-25)
Vertical wing of pelvic girdle	shorter and wider	shorter and wider	narrower and longer	narrower and longer

chiliensis are recognized: *Sarda chiliensis chiliensis* (Cuvier) for the southeastern Pacific population and *Sarda chiliensis lineolata* (Girard) for the northeastern Pacific population (Collette and Chao 1975).

1.24 Standard common names, vernacular names

The common and vernacular names of the species of *Sarda* are given in Table 2.

1.3 Morphology

Collette and Chao (1975) made a detailed study of the morphology of the species of *Sarda* including color pattern, scales, morphometry, meristics, soft anatomy, and osteology.

1.31 External and internal morphology

Sarda australis

Probably in part because of its restricted geographic range there have been no studies on the use of morphological characters to differentiate subpopulations or on the geographic variation in the morphology of *S. australis*. Collette and Chao (1975) presented data on morphometric characters of *S. australis* (Table 3) which give some indication of individual variation in the characters examined.

Sarda chiliensis

Although the temperate northeast (*S. c. lineolata*) and southeast (*S. c. chiliensis*) Pacific populations of *Sarda chiliensis* are completely separated geographically, there are few differences between the two populations and anatomically they are virtually identical (Collette and Chao 1975).

Godsil (1954) presented meristic and morphometric data from the northeast Pacific population of *S. chiliensis*. In a later study, Godsil (1955) also presented similar data for bonitos from the southeast Pacific population and made a comparison of the specimens from the two populations. His conclusion was that such differences as existed between specimens of the northeastern and southeastern populations should be considered as varietal or population differences and that both varieties should be assigned to the same species, *S. chiliensis*.

Collette and Chao (1975) discussed the results of earlier investigators (Walford 1936; Hildebrand 1946; Kuo 1970) who tried to distinguish the two populations by the use of various morphometric characters. They noted that among the meristic characters, the total number of vertebrae was the best character to distinguish the southeast and northeast populations of *S. chiliensis* (Table 4). The mean vertebral count of the northeast population was slightly higher than that of the southeast population. After considering all the published data and their own data, Collette and Chao concluded that "The available data does not convince us that the northeast and southeast Pacific populations are subspecies. However, as the populations are genetically isolated from each other and there are some significant differences, there is practical value in using the available subspecific names, and there is ample historical precedent for the name *lineolata* for the northwest population."

Sarda orientalis

The distribution of *Sarda orientalis* is widespread in the Indo-Pacific and it is likely that independent populations occur in the many different areas where the species is found. Therefore, as Collette and Chao (1975) indicated, subspecific or populational differences are possible.

Silas (1964) gave meristic and morphometric data from *S. orientalis* collected at Vizhingam on the Kerala coast of India. He summarized his data by 5 cm size groups but did not make any conclusions as to any differences in body proportions or meristics in the different size groups. Silas also compared published meristic data on *S. orientalis* from various areas in the Indo-Pacific but refrained from drawing any conclusions on subspecific or populational differences. Based on the scattered material available, Collette and Chao (1975) concluded that there appear to be no significant anatomical or meristic differences between any populations of the species. Morphometric data on *S. orientalis* from Japan and the eastern tropical Pacific are given in Table 5. Godsil (1955) also made detailed morphological studies on *S. orientalis* from the eastern tropical Pacific.

Sarda sarda

A detailed analysis of the geographic variation in *S. sarda* was done by Collette and Chao (1975). They compared *S. sarda* occurring in five geographic areas: North and South America, northeast Atlantic (Scandinavia, Atlantic Europe, and the Azores), Mediterranean Sea (including the Black and Adriatic Seas), and the Gulf of Guinea (extending south to South Africa). They found varying meristic and morphometric differences between and among the populations in the five areas. For example, the meristic characters were similar for the two western Atlantic populations as they were for the Mediterranean and Gulf of Guinea populations. In summary, they concluded that there was at least as much justification for recognition of subspecies in *S. sarda* as in *S. chiliensis*, if names had been available for the populations. They stated that more study is needed on this problem. Morphometric data on *S. sarda* from North America, the Mediterranean, and the Gulf of Guinea are given in Table 6.

Demir (1964) presented meristic data on *S. sarda* from Turkish waters. He found that fin ray counts in the ventral and caudal fins did not vary. However, there were variations in the number of rays in the other fins. He also found variation in the number of vertebrae, gill rakers, and teeth. He computed the mean, standard deviation,

Table 2.—Common and vernacular names of *Sarda* spp.

Species	Country	Standard common names	Vernacular names
Sarda australis	Australia	Australian bonito	Horse mackerel, little bonito
Sarda chiliensis	United States	Pacific bonito	
	Chile	Bonito	
	Peru	Bonito	
Sarda orientalis	Australia (Western)	Oriental bonito	
	India	Oriental bonito	Vari choora (Malayalam)
	Mauritius-Seychelles		Brasse-a-dents (Creole name)
	Somali		Sinufa
	South Africa, Republic of	Bonito	
	Japan	Hagatsuo	Kitsunegatsuo, Hohzan, Sujigatsuo, Sabagatsuo, Shimagatsuo, Tozan
	United States	Bonito	
	Sri Lanka (Ceylon)		Thora-baleya
Sarda sarda	Albania	Palamiti	
	Algeria	Bonite	Bonito, Bonite a dos raye Palamita, Rsela
	Bulgaria	Palamud, Turuk	Lakerda
	Canary Islands	Bonito	Bonite
	Denmark	Rygstribet Pelamide	
	France	Bonite a dos raye	Pelamide commun, Pelamide, Conite, Pelamido, Pelamida, Palamida, Boniton, Bonicou, Bonnicou, Boussicou, Boussicon
	Greece	Palamida, Toriki	Pelamyda, Doriki, Touliki, Ternata, Koini
	Germany	Pelamide	Bonite, Unechter bonito, Mittellandischen bonite, Rygstribed pelamite
	Israel	Sarda	
	Italy	Palamita	Palamita sarda, Pelamida, Palamide, Palamida, Palamita, Palamito, Palamitu maiaticus, Palametto, Pilamitu, Palamia, Paamie, Pirantuni, Pisantuni, Tombarello, Parantuni, Strombo, Strumbo, Scurma, Sangulu, Sgamiru, Sgonfietto, Cuvarita, Cavaritu imperiali, Bonnicou, Tunnachiu
	Libya	Balamit	Blamto
	Madeira Islands	Cerda	
	Malta	Palamit	Plamtu, Palamita, Plamitu, Palamia
	Monaco	Palamida	Piramida, Paramida
	Morocco	Cerda, Bonito	
	Portugal	Bonito, Serra	
	Rumania	Pelamida	Lacherda
	Spain	Bonito	Bonitol, Bonitu, Cerda
	South Africa	Bonito	Katankel, Sarrajoa
	Sweden	Pelamide	Rygstrimmig pelamid
	Syria	Palamet	
	Tunisia	Palamid	Pelamid, Balamit, Toumbrel, Rsela
	Turkey	Palamut, Torik	
	United Kingdom	Pelamid	Belted bonito, Stripe-backed pelamis
	U.S.S.R.	Pelamida	Lacherda
	United States	Common Bonito	Atlantic bonito, Bonito, Boston mackerel, Bone jack, Bloater, Skipjack
	Yugoslavia	Polanda	Polandra, Palovnic, Pastrica, Sarica, Sargasto, Tombarel, Trup lacherda

Table 3.—Morphometric characters of *Sarda australis*. Upper set of numbers are measurements expressed in thousandths of fork length, lower set as thousandths of head length. (From Collette and Chao 1975, table 18.)

Character	Range	$\bar{x}$	N
Fork length (mm)	195-526	349	21
	Fork length		
Snouth — A	662-698	674	20
Snout — 2D	581-605	586	20
Snout — 1D	251-276	263	20
Snout — P_2	281-312	296	20
Snout — P_1	258-281	267	20
$P_1 — P_2$	104-125	116	19
Head length	259-279	267	20
Max. body depth	221-240	231	16
Max. body width	127-169	141	17
P_1 length	112-135	121	19
P_2 length	76-118	85	20
P_2 insertion - vent	340-393	374	18
P_2 tip - vent	260-311	290	18
Base 1D	315-343	326	20
Height 2D	77-95	86	19
Base 2D	88-118	103	20
Height anal	72-92	81	20
Base anal	48-88	78	20
Caudal spread	238-277	259	11
Snout (fleshy)	88-103	96	20
Snout (bony)	76-88	81	20
Maxilla length	131-150	139	20
Post orbital	120-136	130	20
Orbit (fleshy)	32-41	37	19
Orbit (bony)	56-84	66	20
Interorbital width	58-72	66	19
	Head length		
Snout (fleshy)	342-381	361	20
Snout (bony)	291-324	305	20
Maxilla length	503-539	518	20
Post orbital	478-508	492	20
Orbit (fleshy)	134-148	137	19
Orbit (bony)	231-287	246	20
Interorbital width	226-266	249	19

and standard error of the mean for each meristic character with varying counts.

1.33 Protein specificity

See also section 4.14.

Cushing (1964) reported on the use of lectin in the investigation of antigens of tunas and other species. As Cushing pointed out, lectins are not antibodies per se but proteins possessing antibodylike properties. The most well known source of lectin is the seeds of plants of a variety of species. Cushing cited unpublished results of experiments which showed that lectins can be useful reagents in detecting antigens in fishes. The lectin obtained from seeds of a plant, *Dolichos bifloris,* that is routinely used to distinguish the human A_1 subtype was used to show that a significant difference exists between the frequencies of positive fish occurring in samples of *S. chiliensis* of larger and smaller sizes. The cause of this difference has not been determined.

Barrett and Williams (1965) determined the blood hemoglobin level of nine specimens of *S. chiliensis.* The hemoglobin level ranged from 11.2 to 15.3 g/100 ml and averaged 12.9 g/100 ml.

2 DISTRIBUTION

2.1 Total area

The distribution of the four species of *Sarda* as given below and in Figure 2 was adapted from Collette and Chao (1975). The geographic classification and codes given by Rosa (1965) were followed.

Sarda australis

ISEW (Indo-Pacific, central)

610 Australia. 614 Victoria; 615 New South Wales; 616 Queensland; 617 Tasmania; 618 Norfolk Island.

Sarda australis is known only from the east coast of Australia and Norfolk Island. Off the east Australia coast, it is common from about the Capricorns (Queensland) to Sydney or even Gabo Island (Whitley 1964). The westernmost record for the species is from Port Fairy, Victoria (Serventy 1941b).

Sarda chiliensis

INE (Pacific, NE)
ISE (Pacific, SE)

200 North America. 212 British Columbia; 220 Alaska; 231 Washington; 232 California.
300 Latin America. 311 Mexico; 342 Peru; 343 Chile.

This species is found only in the eastern Pacific, where it is separated geographically into north and south temperate populations. The usual range of the northeast population is from about Point Conception, Calif., to Magdalena Bay, Baja California. There is a record of this species from Socorro Island in the Revilla Gigedos. It is uncommon north of Point Conception but it has been recorded from off the Farallon Islands and Eureka, Calif.; off Puget Sound, Wash.; off the east coast of Vancouver Island, B.C., Canada; and in coastal Alaska in Clarence Strait northwest of Ketchikan and off the Copper River.

The range of the southeastern population is along the coast of South America from Mancora, Peru, in the north to Valdivia, Chile, in the south.

Sarda orientalis

ISE (Pacific, SE)
ISEW (Indo-Pacific, central)
ISW (Indian Ocean)

100 Africa. 154 South Africa; 156 Malagasy Republic.

Table 4.—Comparison of morphometric characters in two populations of *Sarda chiliensis*, northeast Pacific (*S. c. lineolata*) and southeast Pacific (*S. c. chiliensis*). Upper set of numbers are measurements expressed as thousandths of fork length, lower set as thousandths of head length. (From Collette and Chao 1975, table 19.)

	Northeast Pacific			Southeast Pacific		
Character	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	207-587	375	24	325-672	498	18
Fork length						
Snout — A	642-674	656	23	631-672	654	18
Snout — 2D	553-595	573	24	551-585	569	18
Snout — 1D	243-281	269	24	268-290	279	18
Snout — P_2	275-318	295	24	280-323	303	18
Snout — P_1	247-279	266	24	260-300	275	18
P_1 — P_2	106-121	112	21	105-131	118	16
Head length	248-275	263	24	259-292	272	18
Max. body depth	179-232	210	19	177-230	210	13
Max. body width	98-167	131	22	116-154	134	10
P_1 length	99-132	116	24	125-152	138	18
P_2 length	65- 87	78	24	65- 91	84	18
P_2 insertion - vent	329-367	353	24	327-368	346	16
P_2 tip - vent	248-331	276	24	237-352	269	17
Base 1D	278-314	297	24	267-303	286	16
Height 2D	64- 98	83	23	82-116	97	17
Base 2D	71-115	93	23	80-109	94	18
Height anal	58- 89	74	23	77-107	92	18
Base anal	61- 84	71	24	61- 88	74	18
Caudal spread	196-300	234	20	228-289	258	11
Snout (fleshy)	87-119	94	24	86-102	95	18
Snout (bony)	71- 83	78	24	75- 89	81	18
Maxilla length	115-136	126	24	121-143	130	18
Post orbital	125-144	139	21	131-150	142	16
Orbit (fleshy)	25- 44	31	24	27- 36	31	18
Orbit (bony)	47- 63	57	22	47- 63	56	18
Interorbital width	57- 69	63	24	62- 82	70	18
Head length						
Snout (fleshy)	339-368	353	23	331-363	348	18
Snout (bony)	283-308	297	24	279-329	299	18
Maxilla length	460-503	481	24	463-489	477	18
Post orbital	499-548	526	21	504-544	523	16
Orbit (fleshy)	102-168	119	24	102-141	115	18
Orbit (bony)	190-238	218	22	174-229	205	18
Interorbital width	213-278	239	24	233-302	257	18

300 Latin America. 311 Mexico; 314 Costa Rica; 315 Panama; 341 Ecuador (Galápagos Islands); 342 Peru.

400 Asia. 423 India; 424 Sri Lanka; 437 Phillippines; 438 Khmer Republic (Cambodia); 451 Japan.

600 Oceania. 612 Western Australia; 660 U.S.A. (Hawaii).

This bonito occurs in widely scattered locations in the Indo-Pacific and Pacific. There is a population of *S. orientalis* in the tropical eastern Pacific that is confined to the coastal areas between the tip of Baja California, Mexico, and Ecuador and around the Galápagos Islands. It occurs in Hawaii but is not common there. In Japan, the species occurs along both coasts of Honshu and is most abundant along the coasts of Kyushu. The species has been recorded from the coast of China and also from the Philippines.

In the Indian Ocean *S. orientalis* has been recorded from southwest Australia, along both coasts of India and from Sri Lanka, from Muscat at the entrance to the Persian Gulf, in the Seychelles Islands and Aldabra Island, and along the coast of Natal, South Africa, south to Durban. It has also been recorded from Eilat at the northern end of the Gulf of Aqaba in the Red Sea.

Sarda sarda

ANW (Atlantic, NW)
ASW (Atlantic, SW)
ANE (Atlantic, NE)
ASE (Atlantic, SE including Bay of Biscay, Mediterranean Sea, Sea of Marmara, Black Sea)

100 Africa. 110 northwestern area; 111 Tunisia; 112 Algeria; 113 Morocco; 114 Canary Islands; 115 former Spanish Sahara; 140 western central area; 141 Islamic Republic of Mauritania; Republic of Senegal, Republic of Guinea; 142 Cape Verde Islands; 144 Ghana; 151 Angola; 152 South-West Africa; 154 Republic of South Africa.

Table 5.—Comparison of morphometric characters in populations of *Sarda orientalis* from Japan and the eastern tropical Pacific. Upper set of numbers are measurements expressed as thousandths of fork length, lower set as thousandths of head length. (From Collette and Chao 1975, table 20.)

	Japan			East tropical Pacific		
Character	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*
Fork length (mm)	342-560	432	7	354-613	472	10
			Fork length			
Snout — A	674-703	694	5	662-703	678	10
Snout — 2D	596-614	606	5	569-596	582	10
Snout — 1D	273-308	286	7	274-311	288	10
Snout — P_2	293-316	303	5	299-321	310	10
Snout — P_1	272-292	281	7	277-299	290	10
P_1 — P_2	109-118	113	5	105-118	114	10
Head length	268-286	278	7	266-294	284	10
Max. body depth	221-244	234	4	193-236	213	10
Max. body width	143-151	146	4	127-153	144	10
P_1 length	104-125	115	7	119-134	127	10
P_2 length	70- 78	76	5	81- 91	86	10
P_2 insertion - vent	374-419	392	7	353-384	367	10
P_2 tip - vent	305-322	311	3	265-302	280	10
Base 1D	285-327	306	7	282-302	292	10
Height 2D	75- 82	78	7	89-101	94	8
Base 2D	85-111	93	7	88-107	95	9
Height anal	61- 85	73	7	84- 97	89	8
Base anal	66- 78	73	7	73- 83	79	9
Caudal spread	168-234	214	4	192-259	236	5
Snout (fleshy)	86-103	96	7	98-105	101	10
Snout (bony)	80- 97	86	7	83- 91	86	10
Maxilla length	141-149	145	6	146-156	150	10
Post orbital	128-147	139	5	141-151	146	10
Orbit (fleshy)	32- 60	42	7	34- 40	37	10
Orbit (bony)	29- 65	56	7	60- 68	64	10
Interorbital width	67- 73	71	6	65- 79	71	10
			Head length			
Snout (fleshy)	306-368	344	7	348-369	357	10
Snout (bony)	288-344	308	7	291-317	303	10
Maxilla length	510-529	522	6	512-557	528	10
Post orbital	476-525	503	5	494-553	512	10
Orbit (fleshy)	102-152	136	7	120-147	130	10
Orbit (bony)	210-234	220	7	210-238	226	10
Interorbital width	251-263	256	6	230-283	251	10

200 North America. 217 Nova Scotia; 235 Southern States; 238 Southern Atlantic States.

300 Latin America. 311 Mexico; 321 Trinidad; 331 Colombia; 332 Venezuela; 351 Brazil; 353 Argentina.

400 Asia. 411 Lebanon; 413 Israel.

500 Europe. 510 Scandinavia; 511 Denmark; 514 Norway; 521 Netherlands; 524 France; 531 Ireland; 534 Scotland; 541 Azores, Madeira; 542 Spain, Balearic Islands; 543 Italy; 553 Greece; 555 Socialist Republic of Romania; 556 Turkey.

700 Union of Soviet Socialist Republic. 710 Crimea.

This bonito is found on both sides of the tropical and temperate Atlantic Ocean, in the Gulf of Mexico, and in the Mediterranean and Black Seas. In the western Atlantic off the east coast of the United States its usual northern limit is Cape Ann, Mass. However, *S. sarda* has been recorded from Casco Bay, Maine, and from several localities along the outer coast of Nova Scotia. It occurs off Florida but is uncommon off Miami and the Florida Keys.

Off the Atlantic coast of South America the species is recorded from Colombia and Venezuela and from about Rio de Janeiro, Brazil, to Buenos Aires, Argentina.

Biogeographical and natural characteristics of areas

No detailed description of the habitat of the four species of *Sarda* will be presented here. From all indications the species of *Sarda* are inhabitants of the coastal or the pelagic neritic province. Sverdrup et al. (1942) set the vertical border separating the neritic from the oceanic province at the edge of the continental shelf. Thus the neritic zone would include all waters of depths <200 m and accordingly may extend far seaward where the continental shelf is wide or may extend only a short distance where the shelf is narrow. "The chemical constituents of the sea water in the neritic province are more

Table 6.—Comparison of morphometric characters in populations of *Sarda sarda* from North America, the Mediterranean Sea, and the Gulf of Guinea. Upper set of numbers are measurements expressed as thousandths of fork length, lower set as thousandths of head length. (From Collette and Chao 1975, table 21.)

	North America			Mediterranean			Gulf of Guinea		
Character	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	228-500	362	17	260-504	376	7	305-443	379	9
				Fork length					
Snout — A	646-690	668	13	641-685	660	7	648-666	657	9
Snout — 2D	570-594	582	13	563-593	579	7	570-585	578	9
Snout — 1D	262-275	270	13	257-284	266	7	262-306	298	9
Snout — P_2	286-304	296	12	280-302	288	6	267-284	275	9
Snout — P_1	259-284	269	13	255-274	263	7	253-273	267	9
P_1 — P_2	105-118	111	12	94-114	104	7	107-118	111	8
Head length	256-272	264	13	251-268	259	7	253-278	271	9
Max. body depth	200-224	214	8	197-216	205	5	195-228	217	8
Max. body width	96-171	135	10	115-148	131	6			
P_1 length	96-138	115	13	105-127	116	6	120-136	130	9
P_2 length	73- 84	79	12	76- 86	82	7	77- 87	83	9
P_2 insertion - vent	348-403	366	13	356-379	370	7	341-388	357	9
P_2 tip - vent	269-302	282	12	269-297	285	7	252-293	266	9
Base 1D	291-330	311	13	301-323	311	7	298-323	311	9
Height 2D	68- 90	80	10	85-117	95	5	81- 99	91	9
Base 2D	85-113	96	13	93-112	104	5	92-112	107	9
Height anal	68- 98	77	11	68- 85	79	6	77- 91	85	9
Base anal	63- 86	73	13	69- 90	78	7	66- 89	80	9
Caudal spread	204-235	222	5	226-270	247	4	223-289	253	3
Snout (fleshy)	76-100	94	13	88- 98	93	7	88-101	96	9
Snout (bony)	78- 93	82	13	74- 83	78	7	75- 85	82	9
Maxilla length	131-141	136	13	127-136	131	7	125-145	138	9
Post orbital	130-142	136	11	126-136	132	7	133-144	138	9
Orbit (fleshy)	27- 40	32	17	27- 34	31	7	31- 36	34	9
Orbit (bony)	35- 64	57	13	53- 62	57	6	53- 64	60	9
Interorbital width	59- 73	64	13	59- 64	62	7	58- 65	63	9
				Head length					
Snout (fleshy)	354-374	360	17	346-367	358	7	346-366	353	9
Snout (bony)	289-342	309	13	289-312	303	7	293-308	301	9
Maxilla	503-529	514	13	497-511	505	7	494-523	509	9
Post orbital	494-541	516	11	503-521	511	7	489-519	506	9
Orbit (fleshy)	100-149	121	17	104-133	118	7	116-132	122	9
Orbit (bony)	203-248	222	16	210-232	220	6	204-228	220	9
Interorbital width	216-275	242	13	231-245	238	7	212-245	231	9

variable than in the oceanic. Salinities are usually lower, sometimes markedly, and undergo seasonal or sporadic fluctuations such that many of the inhabitants are more or less euryhaline in nature—that is, able to endure wide ranges of salinity." (Sverdrup et al. 1942.)

Laevastu and Rosa (1963) determined the distribution of various species of tunas and the temperature range in which the species were found. For the species of bonitos they gave a general temperature range of 12°-25°C and the temperature range of the fisheries for bonitos as 15°-22°C.

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Sarda australis

There is no information on the distribution of fertilized eggs of *S. australis*. The capture of the larvae and juveniles also has yet to be recorded in the literature.

Sarda chiliensis

The distribution of the fertilized eggs of *S. chiliensis* in the eastern Pacific is not well defined. Barnhart (1927) collected bonito eggs in a plankton net off La Jolla, Calif. Orton (1953b) described the early embryonic stage of Pacific bonito but gave no capture locality for her samples. Sokolovskii (1971) made a more detailed study of the distribution of fertilized eggs of the Pacific bonito off Baja California (Fig. 3). As noted by Sokolovskii, *S. chiliensis lineolata* in the spring of 1966 spawned mostly in the shallow waters of the coastal zone. He found fewer fertilized eggs outside the 200 m isobath. He also determined that the eggs are found only at the surface, for no eggs were collected in vertical plankton hauls.

Records of capture of juvenile *S. chiliensis* (Table 7)

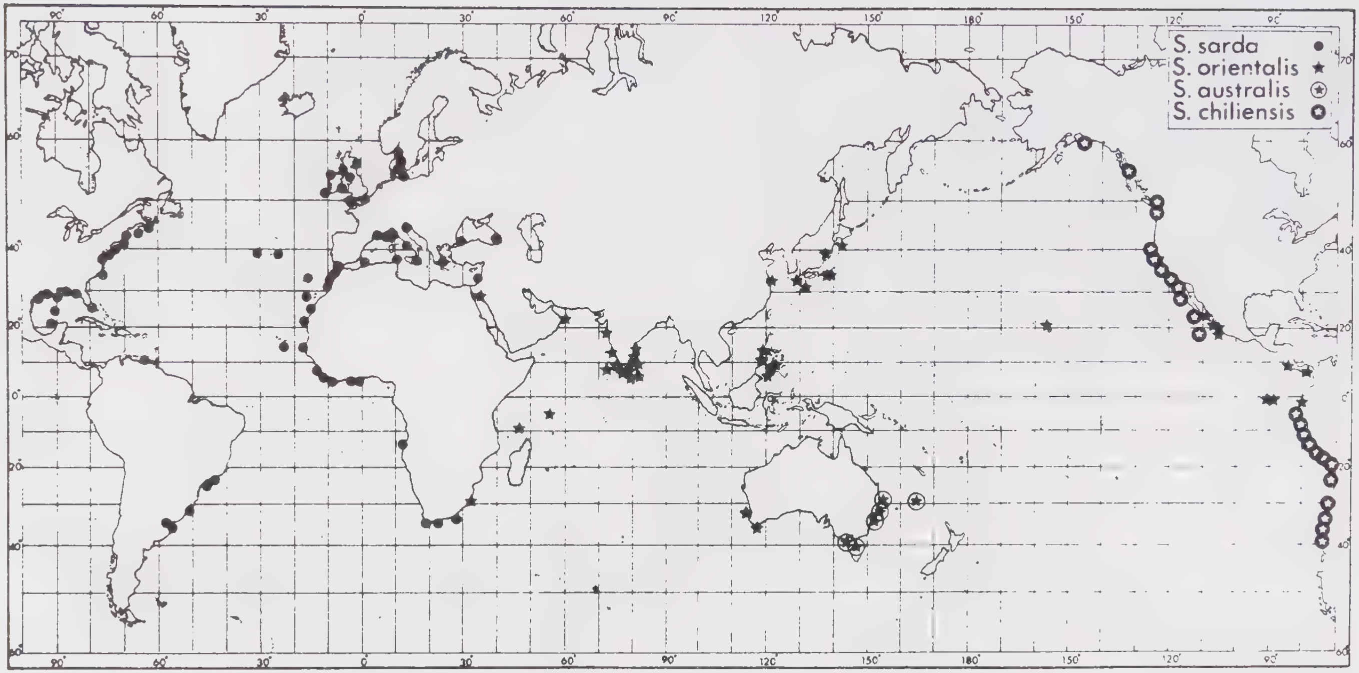
S. sarda ●
S. orientalis ★
S. australis ⍟
S. chiliensis ✪
90°
60°
30°
0°
30°
60°
90°
120°
150°
180°
150°
120°
90°
70°
60°
40°
20°
0°
20°
40°
60°

Figure 2.—Distribution of the four species of *Sarda*. (From Collette and Chao 1975, fig. 70.)

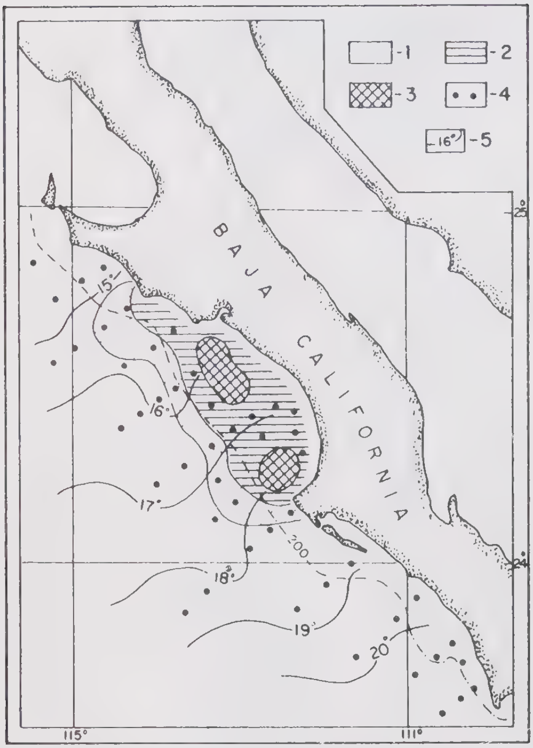

Figure 3.—Distribution of the fertilized eggs of *Sarda chiliensis lineolata* off Baja California in the spring of 1966, based on tows with the ichthyoplankton net. 1—from 1 to 50; 2—from 51 to 500; 3—more than 500 in one tow of the egg net; 4—ichthyoplanktonic stations; 5—isotherms. (From Sokolovskii 1971.)

include two larvae 2.9 and 3.5 mm long; Klawe (1961b) could not determine whether they were *S. chiliensis or S. orientalis.* Other than the prelarval stages which Barnhart (1927) and Orton (1953a, 1953b) reported, and the two larvae recorded by Klawe, the only other larvae of *Sarda* reported from the eastern Pacific are those by Sokolovskii (1971). Sokolovskii reported the capture of six larvae ranging from 7 to 13.8 mm at an ichthyoplankton station in the waters off Baja California. It can be seen from Table 7 that juvenile *S. chiliensis* in the Northern Hemisphere have been found off Baja California between lat. 22° and 26°N. In the Southern Hemisphere they have been found along the coast of Chile and Peru between lat. 13° and 25°S. Vildoso (1966) sampled preadult *S. c. chiliensis* from the Peruvian fishery ranging upward from 20 cm, and Barrett (1971) reported bonito of about 15 cm taken with anchovy catches at Arica, Chile. In southern California, preadult *S. c. lineolata* 15.2-25.4 cm (6-10 in) are first seen by the bait fishermen in the early summer (Frey 1971).

Sarda orientalis

There is hardly any information in the literature on the distribution of the fertilized eggs of *S. orientalis.* Mito (1961) gave generalized descriptions of fertilized eggs of the species in what he termed the Scombrina, including *S. orientalis.* However, Mito gave no capture locality for his samples. Except for this fragmentary bit of information on the planktonic fertilized eggs of *S. orientalis* off Japan, there is nothing on the distribution of their eggs in the other areas of the Pacific and Indo-Pacific where this species occurs.

Records of larval *S. orientalis* are few. Gorbunova (1963) recorded the capture of a larva 11.56 mm long from off the northwest coast of Australia in the Indian Ocean. Elsewhere in the Indian Ocean, Jones (1960) reported specimens 80, 89, 174, and 262 mm in total length from Vizhingam on the west coast of India. In the Pacific Ocean, juveniles ranging in length between 75 and 100 mm are reportedly caught in waters adjacent to southern Kyushu (Yabe et al. 1953), and Kishinouye (1923) reported a specimen 170 mm taken off Wakayama Prefecture, Japan. Juveniles from the stomachs of predators have been recorded from Hawaii (Honolulu Laboratory, Southwest Fisheries Center, unpubl. data.)

Yabe et al. (1953) reported that 75-100 mm *S. orientalis* are caught in waters around southern Kyushu. They also reported on *S. orientalis* landed at the port of Aburatsu, Japan, ranging in size from 161 to 348 mm. Preadult *S. orientalis* occasionally appear in large numbers in the Indian Ocean. Jones (1960) reported large catches of fish ranging in length from 160 to 200 mm off the west coast of India between Trivandrum and Cape Comorin. Gnanamuttu (1966) recorded the occurrence of *S. orientalis* ranging from 240 to 260 mm in total length off the northeast coast of India. In the waters around Sri Lanka the commercial fishery lands fish ranging upwards from 20 cm (Sivasubramaniam 1969).

Sarda sarda

The distribution of fertilized eggs of *S. sarda* has been studied in greater detail in the Black Sea and the Sea of Marmara. Mayorova and Tkacheva (1959) reported on the distribution of *S. sarda* eggs in the Black Sea in 1956 and 1957 (Fig. 4). They noted that in 1956 bonito eggs were found in great numbers in the surface layer, the maximum catch amounting to 12,000 eggs per "10-min catch," presumably made using a plankton net. At a depth of 5 m the number of eggs taken did not exceed 5,000 eggs/10-min tow. In 1957 the overall abundance of fertilized eggs was less than in 1956, and the vertical distribution was also different in that the 5 m depth produced more eggs than the surface layer. Demir (1963) noted that available data indicate that *S. sarda* eggs have been found everywhere in the Black Sea, the locations varying from year to year.

The fertilized eggs of *S. sarda* have also been found in the Sea of Marmara (Fig. 5) (Demir 1963). It can be seen from Figure 5 that in June and July of 1959 most of the fertilized eggs were found in the eastern portion of the Sea of Marmara.

Table 7.—**Records of capture of juvenile *Sarda chiliensis* from the eastern Pacific. (From Pinkas 1961, table 2; Klawe 1961b, table 2, 1962.)**

Date	General locality	Latitude	Longitude	Method of capture	Size range Fork length (mm)	No. of specimens
			Northern Hemisphere			
17-18 May 1947	Off La Jolla, Calif., United States			Night light, dip net	—	1
5 Aug. 1951	100 miles NW of Cape San Lazaro, Baja Calif., Mexico	25°35′N	113°56′W	Night light, dip net	42	1
5 Aug. 1951	Off Baja Calif., Mexico	25°35′N	113°56′W	Night light, dip net	42	1
12 Aug. 1951	Off Ballenas Bay, Baja Calif., Mexico	26°29.5′N	133°29.2′W	Plankton net	2.9, 3.5	1[1]
15 July 1953	South of Cape San Lazaro, Baja Calif., Mexico	23°47′N	112°25′W	Night light, dip net	25-41	5
18 July 1953	Southwest of Cape San Lazaro, Baja Calif., Mexico	23°16′N	112°45′W	Night light, dip net	19-41	8
11 Apr. 1955	South of Cape San Lucas, Baja Calif., Mexico	22°52.8′N	109°53.7′W	Night light, dip net	16.7	1
11 July 1956	Southwest of Cape San Lucas, Baja Calif., Mexico	23°35′N	112°11′W	Night light, dip net	33.0-33.5	2
12 July 1956	Southwest of Cape San Lucas, Baja Calif., Mexico	22°20′N	112°27′W	Night light, dip net	24-48	8
17 July 1956	Southwest of Cape San Lucas, Baja Calif., Mexico	22°47′N	112°14′W	Night light, dip net	54.5	1
5 Apr. 1960	Off Baja Calif., Mexico	23°19′N	110°22′W	High speed net	92	1
			Southern Hemisphere			
20 Feb. 1951	Off Pt. Lobos, Peru			?	125-130	3
3 Jan. 1956	Off Pt. Negra, Peru			Bait net	143-164	3
10 Dec. 1957	Independencia Bay, Peru	14°14′S	76°12′W	Bait net	128	1
13 Dec. 1957	Off Ilo, Peru	17°38′S	71°23′W	Bait net	121	1
15 Dec. 1957	Off Ilo, Peru	17°38′S	71°18′W	Bait net	200.9	1
18 Dec. 1957	Off Ilo, Peru			Bait net	70-135	3
21 Dec. 1957	South of Santa, Peru	09°31′S	78°26′W	Bait net	38.0-51.0	5
31 Dec. 1957	Off Pt. Pichalo, Chile	19°35′S	70°16′W	Night light, dip net	37	1
1 Jan. 1958	Off Ilo, Peru	17°47′S	71°30′W	Bait net	86.8	1
3 Jan. 1958	Off Pt. Dos Reyes, Chile	24°30′S	70°49′W	Night light, dip net	39	1
3 Jan. 1958	Off Pt. Dos Reyes, Chile	24°36′S	71°01′W	Night light, dip net	36-44	3
14 Jan. 1958	Southwest of Fraile Pt., Peru	13°14.8′S	77°55.5′W	Night light, dip net	34	1
Feb. 1958	Off Chimbote, Peru			Bait net	89-129	3
6 May 1958	Almejas Bay, Baja Calif., Mexico			Bait net	103	1
1 Feb. 1959	Sama Cove, Peru			Bait net	111	1
15 Mar. 1959	Off Ilo, Peru			?	135-160	3
16 Mar. 1959	Off Barranca, Peru			?	173, 199	2

[1] Identity uncertain.

It is of interest that very little is known of the distribution of fertilized *S. sarda* eggs in the Mediterranean Sea. Demir and Demir (1961) noted that planktonic fertilized eggs of *S. sarda* were unknown from the Mediterranean Sea. They pointed out that the eggs reported on by Sanzo (1932) were eggs that were extracted from a female gonad and artificially fertilized and reared. More recently, however, Duclerc et al. (1973) reported on the collection of fertilized *S. sarda* eggs near the Balearic Islands in the Mediterranean Sea. Thus, as far as can be determined from the literature, the distribution of fertilized eggs of bonito, is not very well defined in the Mediterranean Sea.

Except for the report of the collection of the fertilized eggs of *S. sarda* off the coast of Massachusetts by Sette (1943), nothing is known of their distribution in the Atlantic Ocean.

Mayorova and Tkacheva (1959) stated that *S. sarda* prelarvae and larvae occur in the same regions as the fertilized eggs in the Black Sea. Figure 4 shows that fertilized eggs of *S. sarda* are widely distributed in the Black Sea, thus indicating that larval bonito are also

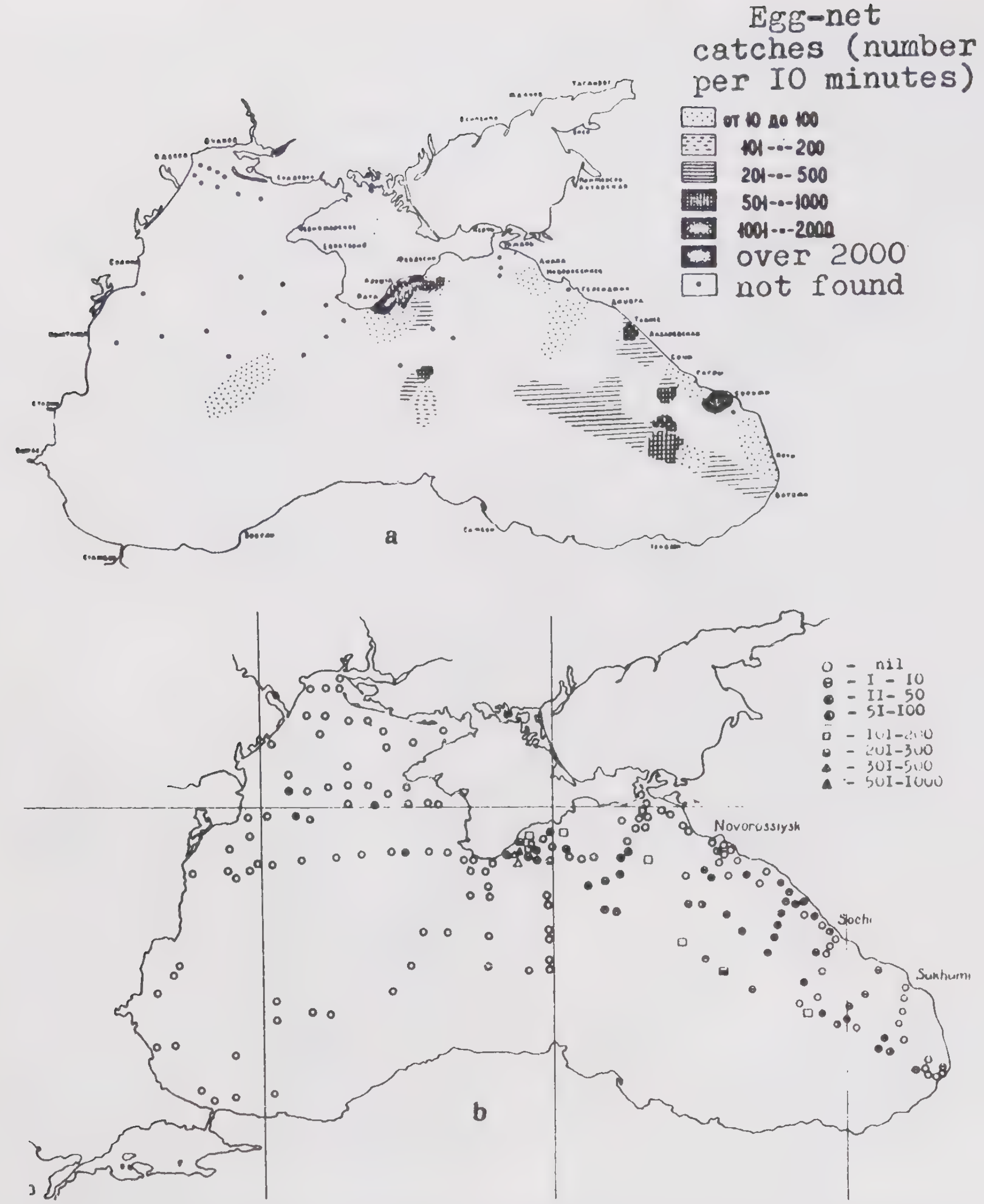
Egg-net catches (number per IO minutes)
от 10 до 100
101---200
201--500
501--1000
1001---2000
over 2000
not found
a
nil
I - 10
II- 50
51-100
101-200
201-300
301-500
501-1000
Novorossiysk
Sochi
Sukhumi
b

Figure 4.—Distribution of the fertilized eggs of *Sarda sarda* in the Black Sea, in June 1956 (a) and June 1957 (b). (From Mayorova and Tkacheva 1959, figs. 1, 2.)

widely distributed. The larvae were more abundant at a depth of 5 m than at the surface. Mayorova and Tkacheva also noted that juvenile *S. sarda* 10-95 mm long were distributed over a vast area of the Black Sea in waters from 80 to 100 miles from the coast. In the Sea of Marmara, however, plankton tows did not reveal any *S. sarda* larvae although fertilized eggs in all stages of development were plentiful (Demir 1963).

Elsewhere, larvae of *S. sarda* have been reported from the Mediterranean Sea northwest of Oran by Ehrenbaum (1924) and in the Alboran and Mediterranean Seas by Buen (1930, 1932). More recently, freshly hatched

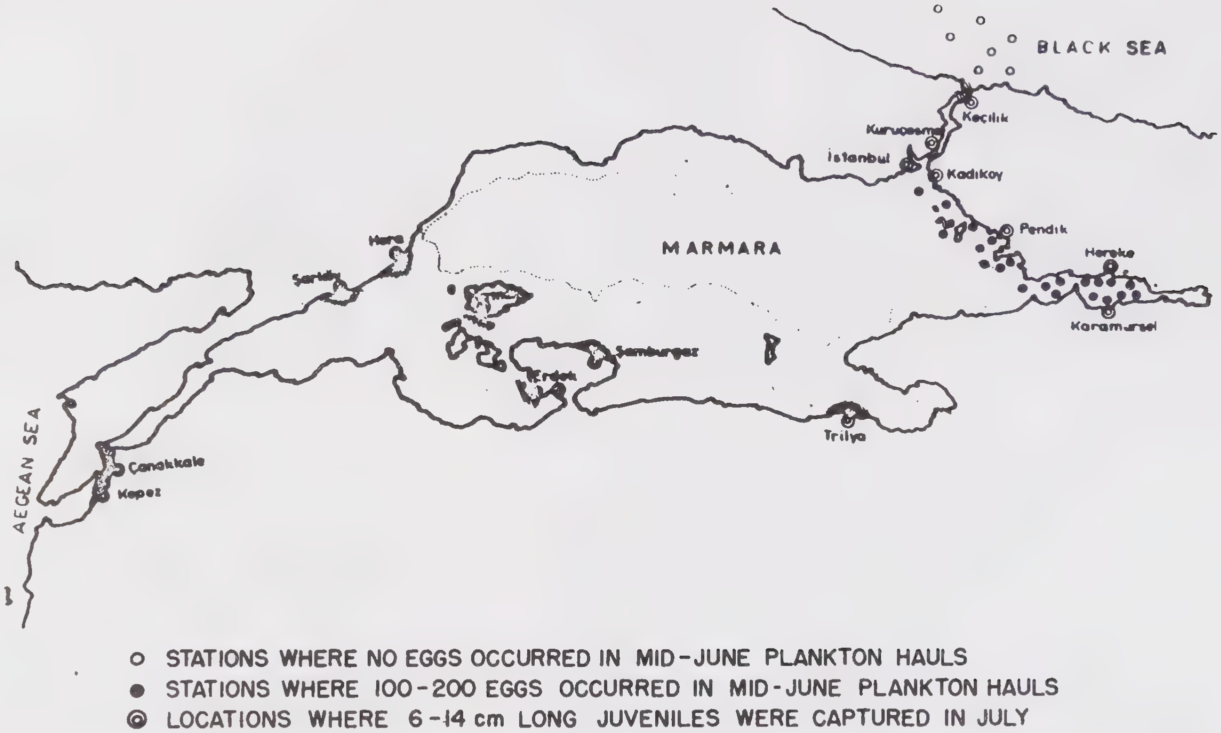
BLACK SEA
MARMARA
AEGEAN SEA
Keçilik
Kuruçeşme
İstanbul
Kadıkoy
Pendik
Hereke
Karamursel
Trilya
Hora
Erdek
Çanakkale
Kepez
○ STATIONS WHERE NO EGGS OCCURRED IN MID-JUNE PLANKTON HAULS
● STATIONS WHERE 100-200 EGGS OCCURRED IN MID-JUNE PLANKTON HAULS
◎ LOCATIONS WHERE 6-14 cm LONG JUVENILES WERE CAPTURED IN JULY

Figure 5.—Distribution of the fertiized eggs of *Sarda sarda* in the Sea of Marmara, June and July 1959. (From Demir 1963, fig. 3.)

prelarvae were collected near the Balearic Islands by Duclerc et al. (1973). In the Atlantic Ocean, larvae have been found off Cuba (Gorbunova and Salabarría 1967), and a juvenile measuring 34 mm has been recorded off the South Carolina coast (Klawe 1961a). Two juvenile *S. sarda* 64 and 67 mm in total length were also captured in the Gulf of Mexico (Klawe and Shimada 1959).

Sarda sarda from 6 to 18 cm long are captured in varying numbers in the Dardanelles, the Bosporus, the Sea of Marmara, and the Black Sea nearly every year in July-August (Demir 1963). The abundance of preadults in this size range apparently is a good indicator of the future abundance of fish 25-38 cm long which are the basis of an important Turkish fishery that takes place starting in September in the same areas. Preadults 8-12 cm long have been captured in large numbers in the Aegean Sea (Serbétis 1955), and Belloc (1954) discussed the occurrence of *S. sarda* 7.5-20 cm long caught in the Gulf of Naples and the Gulf of Catania and 15-25 cm long fish in the Bay of Biscay.

The capture of preadults 20-30 cm long has been reported from the Atlantic coast of France (De la Tourrasse 1957), and 25-35 cm fish have been taken commercially together with mackerel in the Miramichi estuary in the Gulf of St. Lawrence (McKenzie 1959). Klawe and Shimada (1959) reported the capture of two specimens 64 and 67 mm long in the Gulf of Mexico. Young *S. sarda* 12.7-15.2 cm (5-6 in) long have been taken off Orient, N.Y. (Nichols and Breder 1927).

2.22 Adults

Sarda australis

Information on the seasonal and annual variations in the occurrence of *S. australis* on the east coast of Australia is fragmentary. Serventy (1941b) stated that this species apparently is only a summer visitor to Victoria. Munro (1958) noted that *S. australis* was more plentiful north of Sydney in the winter; and according to Grant (1972), it commonly occurs in schools in inshore waters of Queensland, especially in winter. However, Marshall (1964) stated that *S. australis* is very common on the coasts of Queensland and New South Wales and is found in great schools throughout the year.

Sarda chiliensis

For the northeast population of *S. chiliensis* MacCall et al. (1976) suggested an uneven geographical distribution of various age groups. They noted that, roughly, older fish were more available offshore and around Mexico although large fish were also taken in the Santa Barbara, Calif., area in the fall.

As for the southeast population of *S. chiliensis,* Ancieta (1963) found that off the coast of Peru 82.2% of the total landings during 1951-60 were made in the central zone, from Chimbote to Pisco; 11.8% were made in the southern zone, from San Juan to Ilo; and 6% were made in the northern zone, from Máncora to Salaverry. However, Mejía et al. (1971)[3] noted that beginning in 1962 there has been a gradual overall decline in the annual Peruvian landings of *S. c. chiliensis,* most notably at the central zone port of Callao; in contrast the landings at the northern zone port of Paita increased somewhat.

Off the Chilean coast *S. c. chiliensis* are taken from the northern boundary of Chile to as far south as Talcahuano, but most are taken off the northern ports of Arica, Iquique, and Antofagasta, especially between Iquique and Mejillones (Barrett 1971). It was also seen that almost two-thirds of the annual Chilean landings of *S. c. chiliensis* are made in the last third of the year.

Sarda orientalis

Along the southwest coast of India, fully mature adult *S. orientalis* are found from May to September followed by the juveniles from October to November. Slight annual fluctuations in seasonal occurrence are also seen (Silas 1964).

Off the south coast of Sri Lanka (Ceylon), *S. orientalis* appears in the commercial catches throughout the year. Mature fish are taken off the south and southwest coasts primarily between September and February, and the juveniles appear off the west coast more often from June to August (Sivasubramaniam 1969). Generally, *S. orientalis* appears in the commercial catches most frequently off the south coast, to a lesser extent off the west and northwest coasts, and least frequently off the southwest and northeast coasts.

Sarda sarda

The seasonal occurrence of *S. sarda* in various localities is summarized in Tables 8 and 9.

2.3 Determinants of distribution changes

Along the California coast there appears to be a relationship between the latitudinal distribution of *S. chiliensis* and sea temperature (Radovich 1963). An upsurge in the average daily *S. chiliensis* catch of partyboat anglers took place with the onset of a warmwater period off California in 1957. Radovich suggested that *S. chiliensis* moved northward into California waters during warm years. He also noted that during warm years, bonitos spawned successfully in California waters, thus further increasing the local population.

From all indications it appears that all the species of *Sarda* are closely associated with the coast, where the ocean environment may be subject to rapid changes. Demir (1963) stated, however, that *S. sarda* cannot tolerate sudden changes in environment, but they can adapt to gradual changes in temperature ranging from 12° to

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[3] Mejía, J., M. Samamé, and A. de Vildoso. 1971. Revisión de la pesquería del bonito en quas Peruanas. Fourth Session of FAO Panel of Experts for the Facilitation of Tuna Research, La Jolla, Calif., 8-13 November 1971. (Mimeogr.)

Table 8.—Fishing seasons for *Sarda sarda.*

Area	Fishing season	Peak months of fishing	Source
Black Sea	May-October	—	Demir (1963)
Bosporus, Sea of Marmara, Dardanelles	Throughout the year	April-May, September-December	Demir (1963)
Aegean Sea (around Greece)	Throughout the year	—	Serbétis (1955)
Eastern Mediterranean (off Spain)	May-June	—	Gruvel (1931)
Mediterranean (off Tunisia)	Throughout the year	May-July	Postel (1955b)
Eastern tropical Atlantic	October-May	—	Postel (1955b)
Eastern Atlantic (off Morocco)	Throughout the year	—	Furnestin et al. (1958)
Eastern Atlantic (Bay of Biscay)	Mid-April to mid-May	—	de la Tourrasse (1957)
Western Atlantic (Gulf of Maine)	June-October	—	Bigelow and Schroeder (1953)

Table 9.—Fishing seasons in the Spanish fishery for *Sarda sarda.* (From Rodrıguez-Roda 1966, table 2.)

Area	Fishing season	Peak months of fishing
Bay of Biscay (along Spanish coast)	April-November	July-October
Eastern Atlantic (off northwest coast of Spain)	April-December	July, August
Eastern Atlantic (southwest coast of Spain)	January-December	September, October
Western Mediterranean (southeast coast of Spain)	January-December	August-October
Western Mediterranean (east coast of Spain)	January-December	May, September
Western Mediterranean (northeast coast of Spain)	January-December	June-November
Western Mediterranean (Balearic Islands)	January-December	May-September
Eastern Atlantic (Canary Islands)	January-December	August, September

27°C and salinities between 14 and 39‰. *Sarda sarda* have been taken in the Miramichi estuary, Gulf of St. Lawrence, where the condition must surely be less than oceanic. *Sarda orientalis* have been found in waters ranging from 13.5° to 23°C (Kishinouye 1923).

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

All four species of *Sarda* are usually heterosexual, and there are no apparent external anatomical differences between the males and females. In *Sarda c. lineolata,* however, Magnuson and Prescott (1966) noted a sexual dimorphism in the behavior of this species in captivity. Magnuson and Prescott noted that some *S. c. lineolata* in their observation tank were "wobblers" and that others were "followers." They postulated and subsequently determined that the "wobblers" were females and the "followers" were males. They also determined by their observations that a male bonito was apparently unable to identify the sex of another bonito except by behavioral characteristics. The bonito is normally heterosexual; however, Vildoso (1960) found cases of hermaphroditism in *S. c. chiliensis* in Peruvian waters. It is of interest that Magnuson and Prescott observed that one fish exhibited both a "wobbling" and "following" behavior. They attributed the anomalous behavior of this particular fish to a possible misidentification and did not speculate on the possibility of hermaphroditism or other causes for the aberrant behavior.

As is the case with the other species of bonitos, the sexes cannot be distinguished in *S. sarda.* Apparently, however, some Turkish fishermen can distinguish the sexes by rubbing the skin anterior of the anus with a fingertip. The skin is said to be smooth in the females and rough like emery paper in the males (Demir 1963).

3.12 Maturity

Sarda australis

The literature contains very little information on *Sarda australis.* Serventy (1941b) reported on three fish caught in January and February 1939 off Wilson's Promontory and Port Albert. The fish weighed between 1.8 and 2.3 kg (4 and 5 lb); and two, which were females, had "relatively large roes." Whitley (1964) noted that *S. australis* sometimes venture into Victoria in the summer (January to April) and that some of these fish had large roe. He also found that fish ready to spawn were found in February and March off New South Wales.

Sarda chiliensis

Barrett (1971) determined the gonad index (GI) ($GI = \frac{\omega}{W} \times 10^2$, where w = weight of both ovaries in grams and W = body weight in grams) of bonitos and found that female *S. c. chiliensis* off the coast of Chile initially reached sexual maturity at a length of 51 cm. For the bonitos off the coast of Peru, Vildoso (1966) determined that the size at first spawning ranged from 47 to 53 cm. Kuo (1970) stated that in the Northern Hemisphere population of *S. chiliensis,* the females attained sexual maturity at 51 cm and that the fish was 5 yr old at that length.

Sarda orientalis

Although the size of *S. orientalis* at first spawning has not been clearly determined, a 38.6 cm specimen possessed residual eggs which were presumably remnants from an earlier spawning (Silas 1964). However, Silas indicated that specimens in "ripe running condition or had already spawned, some showing signs of recovery" measured between 480 and 605 mm from samples collected in 1960 and 1961 at Vizhingam, India. The age of these specimens was not determined. Rao (1964) found four specimens ranging in size from 48 to 55 cm with running-ripe ovaries in June, August, and September 1959, also from Vizhingam.

Sarda sarda

The bonito in the Sea of Marmara and the Bosporus usually attain sexual maturity at the end of the second year, although in some years they may be sexually mature in a year. Two-year-old fish range from 52 to 57 cm and 1-yr-old fish from 42 to 48 cm.

In the Black Sea, part of the stock of *S. sarda* attains sexual maturity in the second year of life. These 2-yr-old fish are said to vary from 33 to 50 cm. Off the coast of Dakar in the eastern Atlantic, the size at first maturity is 392 mm for the males and 370 mm for the females. These fish are less than a year in age.

3.13 Mating

As Magnuson and Prescott (1966) pointed out, pelagic schooling fish were assumed to have no discrete courtship behavior and no pairing and were believed to shed eggs and sperm promiscuously while gathered in large active schools. To the contrary, Magnuson and Prescott found that *S. c. lineolata* do exhibit courting and pairing behavior, if only temporarily, and observed pairs of fishes in a sequence of behavior leading to a simultaneous and adjacent release of eggs and milt. The pair of bonitos released the gametes during a circle swimming behavior in which the male swam in tandem with the female in a circular path.

Although some behavioral patterns have been observed only in *S. c. lineolata,* it would not be unreasonable to expect that the other species of *Sarda* also behave in a similar manner.

3.14 Fertilization

External in all four species of *Sarda.*

3.15 Gonads

Sarda australis

No information.

Table 10.—Fecundity of *Sarda sarda*.

Area	Size of fish	Fecundity (No. of eggs)	Reference
Black Sea	40-50 cm 60-70 cm 70 cm	700,000-1,000,000 1,500,000-2,000,000 6,000,000	Zusser (1954)
Black Sea	—	450,000-1,000,000	Slastenenko (1956)
Black Sea	—	700,000-1,000,000	Krotov (1957)
Black Sea	56-65 cm (2-3.8 kg)	732,160-3,233,580	Mayorova and Tkacheva (1959)
Eastern Atlantic	60 cm	900,000	Postel (1955a)

Sarda chiliensis

Vildoso (1963a) estimated the number of ova spawned by a 600 mm (3 kg) bonito at half a million per spawning season. According to Vildoso, spawning is fractionary. Kuo (1970) estimated that the fecundity of the northern *S. chiliensis* ranged from 104,900 to 894,200 eggs for fish from 47.6 to 63.7 cm in fork length. He indicated that the fecundity increased exponentially with size of fish.

Sarda orientalis

Silas (1964) made fecundity estimates for five mature specimens of *S. orientalis* from the Indian Ocean. He estimated that the females produce 0.08-0.15 million eggs/spawning and 0.24-0.64 million eggs/spawning season. Rao (1964) estimated that the bonito spawns 0.21-0.28 million eggs/spawning and 0.91-1.15 million eggs/spawning season in the Indian Ocean.

Sarda sarda

Demir (1963) summarized the fecundity determinations for *S. sarda* made by various investigators in the eastern Atlantic (Table 10). The fecundity estimates range from 450,000 to over 3,000,000 eggs.

3.16 Spawning

Sarda australis

Whitley (1964) indicated the occurrence of fish that were ready to spawn in February.

Sarda chiliensis

The spawning season for *S. c. chiliensis* in Chilean waters begins in September, is at a maximum in October and November, and is well over before April (Barrett 1971). The spawning season off the coast of Peru is very similar to that off Chile; peak spawning of bonito extends from October to February (Vildoso 1966). According to both authors, larger, older bonito mature earlier in the spawning season than do the younger fish (Fig. 6).

For the Northern Hemisphere population of *S. chiliensis,* Kuo (1970) investigated several different approaches to determine the spawning season, including

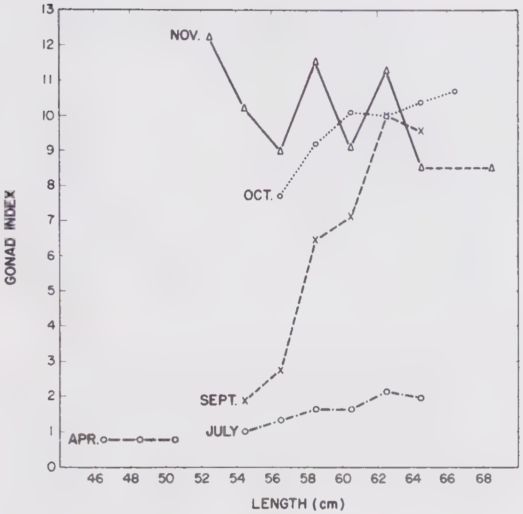

Figure 6.—Mean monthly gonad indices, $GI = \frac{w}{W} \cdot 10^2$, by length class, of female *Sarda chiliensis chiliensis* sampled from the commercial landings at Iquique, September 1968 to July 1969. (From Barrett 1971, fig. 5.)

the annual cycle in the development of intraovarian oocytes, the annual cycle of frequency distribution of ovum diameters, and the annual change in gonad index. All of the different methods indicated that the spawning season for the Northern Hemisphere *S. chiliensis* in southern California is from May through July. Kuo speculated that off southern Baja California spawning may start as early as April and may continue into August. He also indicated that the larger fish tend to spawn earlier in the season and longer than the smaller fish. Frey (1971), however, attributed an early spawning season to *S. c. lineolata* between southern California and northern Baja California waters. He stated that the bonitos spawned between January and May in these waters.

The results of an ichthyoplankton survey off Baja California seem to corroborate the conclusions of Kuo (1970). On the basis of the distribution of fertilized eggs, Sokolovskii (1971) showed that *S. c. lineolata* spawned in a relatively large area near the coast (Fig. 3). In early March the most intensive spawning occurred in the southern area and in early April it occurred in the northern area. The depth of the ocean in the spawning area ranged from 40 to 150 m, and practically no bonito eggs were found outside of the 200 m isobath. Larval bonito were captured at only one station during this survey.

Most of these observations tend to support Klawe (1961b) who, on the basis of the capture of larval and juvenile *S. chiliensis,* had stated that the spawning of this species takes place in the warmer season off California, Baja California, Peru, and northern Chile.

Evidence has also been gathered which suggests that 1- and 2-yr-old *S. c. lineolata* spawn in areas influenced by warmwater discharges during spawning periods when the water is cold. Tag returns have shown that small numbers of young fish stay in these areas for as long as 2 yr and provide a small amount of recruitment even in cold years (Collins and MacCall 1977).

Sarda orientalis

The literature contains very little information on *S. orientalis* spawning in the eastern Pacific and around Hawaii. Klawe (1961b) reported on two larval forms of *Sarda* from off Baja California that could not be identified to species. The distribution of the northeast population of *S. chiliensis* overlaps or nearly overlaps that of the population of *S. orientalis* at the location of capture of the larvae; therefore, the larvae could be either of the two species.

Nothing is known about the spawning of *S. orientalis* around Hawaii except that a few juveniles have been found in the stomachs of predators (Honolulu Laboratory, Southwest Fisheries Center, unpubl. data), which provides evidence of reproduction.

No formal studies on the spawning of *S. orientalis* in Japanese waters have been made. Kikawa and Staff of the Nankai Regional Fisheries Research Laboratory (1963) presumed that spawning occurs in the coastal waters of the tropical zone in the Indo-Pacific. There apparently is some local unrecorded knowledge of bonito spawning in Japan because Harada et al. (1974) reported that the spawning season is May-June. They caught mature *S. orientalis* on 15 May and 10 June in traps set near the coast of Oshima Island and used these fish successfully in an artificial fertilization experiment. Mito (1961) gave descriptions of the fertilized eggs of *S. orientalis* found in plankton collections but gave no collection details. Kishinouye (1923) and Yabe et al. (1953) reported on the capture of juvenile bonito in southern Honshu and Kyushu waters.

Off the coast of Vizhingam in the Indian Ocean, *S. orientalis* spawn from April to September and possibly in other months of the year. Ova diameter frequency distributions indicate the possibility that individual females spawn several batches of ova (Fig. 7) during the spawning season (Silas 1964).

Gorbunova (1963) reported on the larva of *S. orientalis* from the Indian Ocean off the northwest coast of Australia and generalized that spawning is limited to the autumn-winter period. However, this conclusion is based, apparently, on the capture of one larva of *S. orientalis* in December. Gorbunova probably has the seasons confused, for December off the northwest coast of Australia would be closer to summer in the Southern Hemisphere.

Sarda sarda

Demir (1963) stated that *S. sarda* spawning begins in mid-May, reaches a peak in June, and lasts at least to the end of July. He assumed that the spawning season is the same in the Black, Marmara, and Aegean Seas.

Indications are that the spawning season in the Medi-

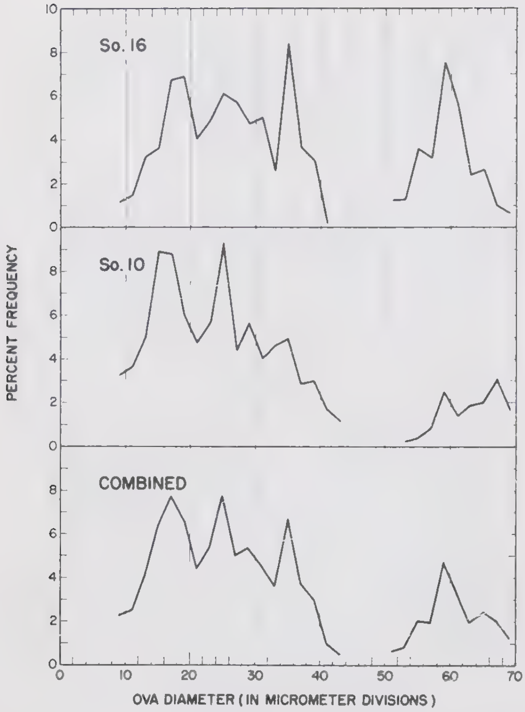

Figure 7.—Ova diameter-frequency polygons of ripe ovaries of the oriental bonito, *Sarda orientalis*, from the southwest coast of India. The ripe ova were sampled from two of four ripe fish examined from June to September 1959. (From Rao 1964, fig. 3.)

Table 12.—Relation between the stage of sexual maturity and the gonadosomatic index ($GI = \frac{w}{W} \cdot 100$, where w is gonad weight and W is fish weight) for *Sarda sarda* landed at Barbate, Spain in 1964. (From Rodríguez-Roda 1966, table 26.)

Stage of sexual maturity	Males			Females		
	Mean	Range	No. of fish	Mean	Range	No. of fish
I (immature)	—	—	—	0.56	0.42-0.69	2
II (early maturing)	0.94	—	1	0.85	—	1
III (mature)	4.15	0.96-6.90	30	4.44	1.77-12.15	23
IV (prespawning)	—	—	—	5.39	3.56-9.40	8
V (spawning)	–	—	—	—	—	—
VI (spent)	—	—	—	2.15	—	1

terranean is also from May to July. However, Demir (1963) noted that Dieuzeide et al. (1955) found that the spawning season off the coast of Algeria is from March to May.

Rodríguez-Roda (1966) made observations on the sexual development of *S. sarda* landed in May, June, and July 1963 and 1964 in the Spanish fishery based at the Mediterranean ports of Barbate and Tarifa. By gross examination of the gonads, he classified the males and females according to six stages of sexual maturity: I, Immature; II, Early maturing; III, Mature; IV, Prespawning; V, Spawning; and, VI, Spent. Data on the monthly percentage distribution of fish in the various stages of sexual maturity were given by Rodríguez-Roda (Table 11). He also computed the *GI* of the fish for his 1964 samples using the equation $GI = \frac{w}{W} \cdot 100$, where w is the weight of the gonads and W is the weight of the fish, and determined the relation between the stage of sexual maturity and the *GI* (Table 12). Rodríguez-Roda noted that the smallest fish with prespawning and spawning gonads were 39.5 cm for the males and 40.5 cm for females.

In the eastern Atlantic near the coast of Dakar the spawning season extends from December to June, including peaks in January and April, and June to July in Moroccan waters. Less is known about *S. sarda* spawning in the western Atlantic. Bigelow and Schroeder (1953) stated that the bonito spawns south of the Gulf of Maine in June. However, Sette (1943) reported the collection of bonito eggs near Martha's Vineyard, Mass., in July. Further south off the South Carolina coast Klawe (1961a), based on the capture of a singe 34 mm bonito, stated that this species spawns in the winter. The capture of a larval bonito (Gorbunova and Salabarría 1967) off the coast of Cuba and a juvenile specimen in the central Gulf of Mexico (Klawe and Shimada 1959) indicates some spawning activity in these areas.

3.17 Spawn

The fertilized eggs of the bonitos have been described for all the species in the genus except *Sarda australis*. Except for differences in size, the fertilized eggs at the various developmental stages appear to be quite similar, and it is doubtful if the species could be separated. As examples of differences in size of the fertilized eggs among the species of *Sarda*, Demir (1963) found that for *S. sarda* in the Sea of Marmara, the eggs, which were measured after preservation in 4% Formalin, varied between 1.18 and 1.55 mm in diameter. The fertilized eggs of *S. c.*

Table 11.—Monthly percentage distribution of *Sarda sarda* in the various stages of sexual development, Barbate and Tarifa, Spain, in 1963 and 1964. (I, immature; II, early maturing; III, mature; IV, prespawning; V, spawning; VI, spent.) (From Rodríguez-Roda 1966, table 24.)

	Males							Females						
	I	II	III	IV	V	VI	No. of fish	I	II	III	IV	V	VI	No. of fish
May	7.02	1.75	87.72	3.51	—	—	57	30.00	15.00	55.00	—	—	—	20
June	—	—	73.81	23.81	2.38	—	42	2.38	—	64.29	30.95	—	2.38	42
July	—	—	100.00	—	—	—	18	—	—	54.17	41.67	—	4.17	24

lineolata from off the coast of Baja California measured from 1.4 to 1.8 mm in diameter (Sokolovskii 1971). However, no mention is made of whether the eggs were measured before or after preservation. Harada et al. (1974) reported that the fertilized eggs of *S. orientalis* were from 1.32 to 1.45 mm in diameter. Here again it is not clear whether the eggs were measured fresh or after preservation. These fertilized eggs were the result of a successful experiment in artificial fertilization, the first record of success in artificial fertilization for this species.

Because the fertilized eggs of the species of *Sarda* are similar in appearance, as a typical example Demir's (1963) description of the eggs (Fig. 8) of *S. sarda* is given below.

The fertilized planktonic eggs of *S. sarda* are spherical, transparent, and, except for the oil globule, colorless. The yolk sac is homogeneous and finely granulated, and varying numbers of oil globules of different sizes are present on its surface.

Although yellow and black pigmentation are present on the developing embryo, only the black pigments (melanophores) remain after preservation. The melanophores on the yolk are found on the surface of the sac. On the embryo they initially appear on the dorsal part of the body and later on the head and tail.

3.2 Preadult phase

3.21 Embryonic phase

See section 3.17.

3.22 Larvae and adolescent phase

The size of a newly hatched larva of *S. chiliensis* is given by Barnhart (1927) as 3.75 mm. Newly hatched larvae of *S. orientalis* measured 4.1-4.3 mm (Harada et al. 1974). As a typical example of the development of the larvae of bonitos, a description of the larval and postlarval development of *S. sarda* is given below. The description is taken from a translation of Padoa (1956).

Embryonic development is rapid and the larva hatches only a day after the closure of the blastopore.

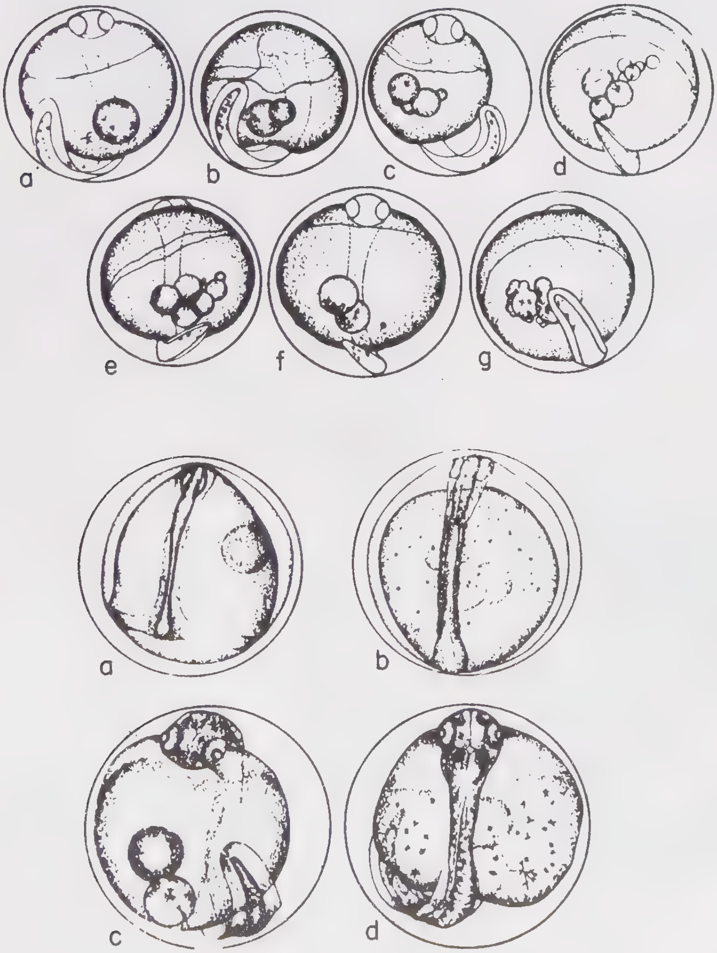

Figure 8.—The fertilized eggs of *Sarda sarda* at various developmental stages. (Note: The developmental stages were not defined by the authors.) (From Demir and Demir 1961.)

The mouth of the larva is not yet open, and the eye without pigment at hatching (Fig. 9a). The yolk sac and fin folds are large, and several oil droplets are present in the posterior part of the yolk sac. The anal opening is located a little less than midway between the head and tail. The pectorals are barely outlined. There is a total of about 50 body segments, including 15 preanal and 38 postanal segments.

The yolk is reduced to less than half in a 4.6 mm specimen 2 days after hatching (Fig. 9b). The mouth is open, the anus has moved forward, and the number of preanal segments is decreased from 15 to 11 and the postanal increased to 39. The pectorals are well developed and membranous; the hypurals are absent. Melanophores on the trunk are limited to the caudal ventral margin; other melanophores are present in the curve of the peritoneal cavity and a few are found on the profile of the snout.

The yolk is nearly used up in a 4.68 mm specimen 4 days after hatching (not illustrated). The snout is considerably longer and there are well-defined teeth. There is a posteriorly directed triangular spine at the preopercular margin. The anus is displaced even farther forward to about the 9th segment. The pectorals are unchanged and the hypurals are still absent. The melanophores persist on the caudal ventral margin; the number and size of melanophores are increased on the dorsal peritoneal walls and the head.

The yolk is exhausted in a 4.20 mm specimen 6 days after hatching (Fig. 9c). The snout is a little more distinctly pointed and is changing to the subconical form. The preopercular spine is pointed and evident; the preanal distance is about 34% of the total length. The pectorals are membranous and the rounded margin reaches about the level of the anus; the hypurals are still absent. There are a few irregularly spaced melanophores on the ventral margin of the trunk. The melanophores persist on the peritoneal curve, along the thoracic girdle, and on the upper profile of the head; they are also present at the apex of the snout and in the middle of the mandible.

Melanophores are present on the apex of the snout, on the profile of the head, on the peritoneal curve, and along the thoracic girdle in a 7.2 mm specimen (Fig. 10c). Black pigments are almost completely lacking on the caudal trunk and limited to a few dispersed elements along the ventral margin. Two series of preopercular spines (an anterior of three and a posterior of six), of which the two central ones are very long, are now developed; two other spines are present on the posterior margin of the otocysts. About 10 pointed teeth are on each side of the maxillary and the mandible. Outlines of about 13 rays, the future second dorsal and anal fins, can be counted. The preanal distance now represents 42% of the total length and the distance from the snout to the

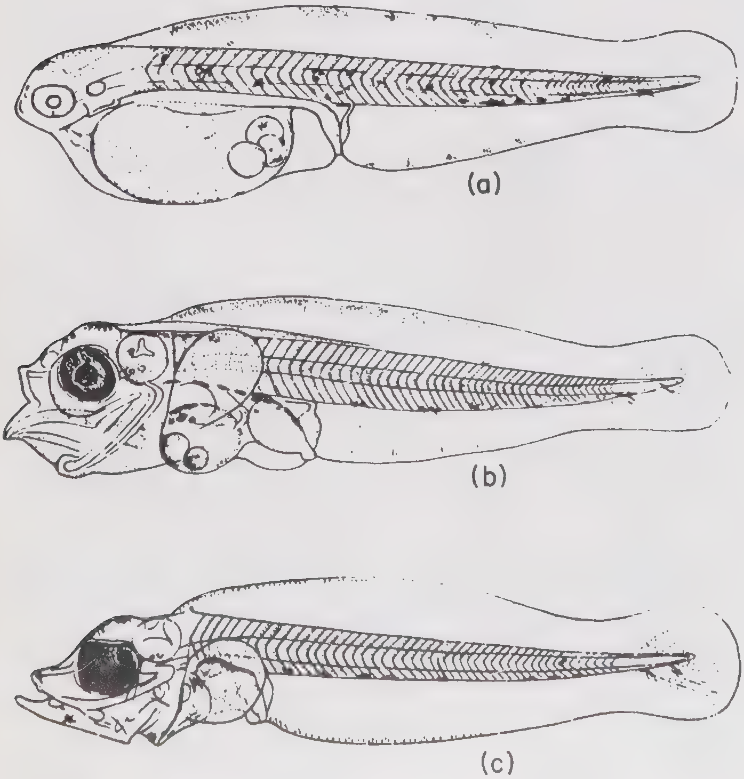

Figure 9.—Prelarvae of *Sarda sarda*: (a) 4.32-mm prelarva (from Padoa 1956, fig. 309); (b) 4.6-mm prelarva (from Padoa 1956, fig. 310); (c) 4.20-mm prelarva (from Padoa 1956, fig. 311).

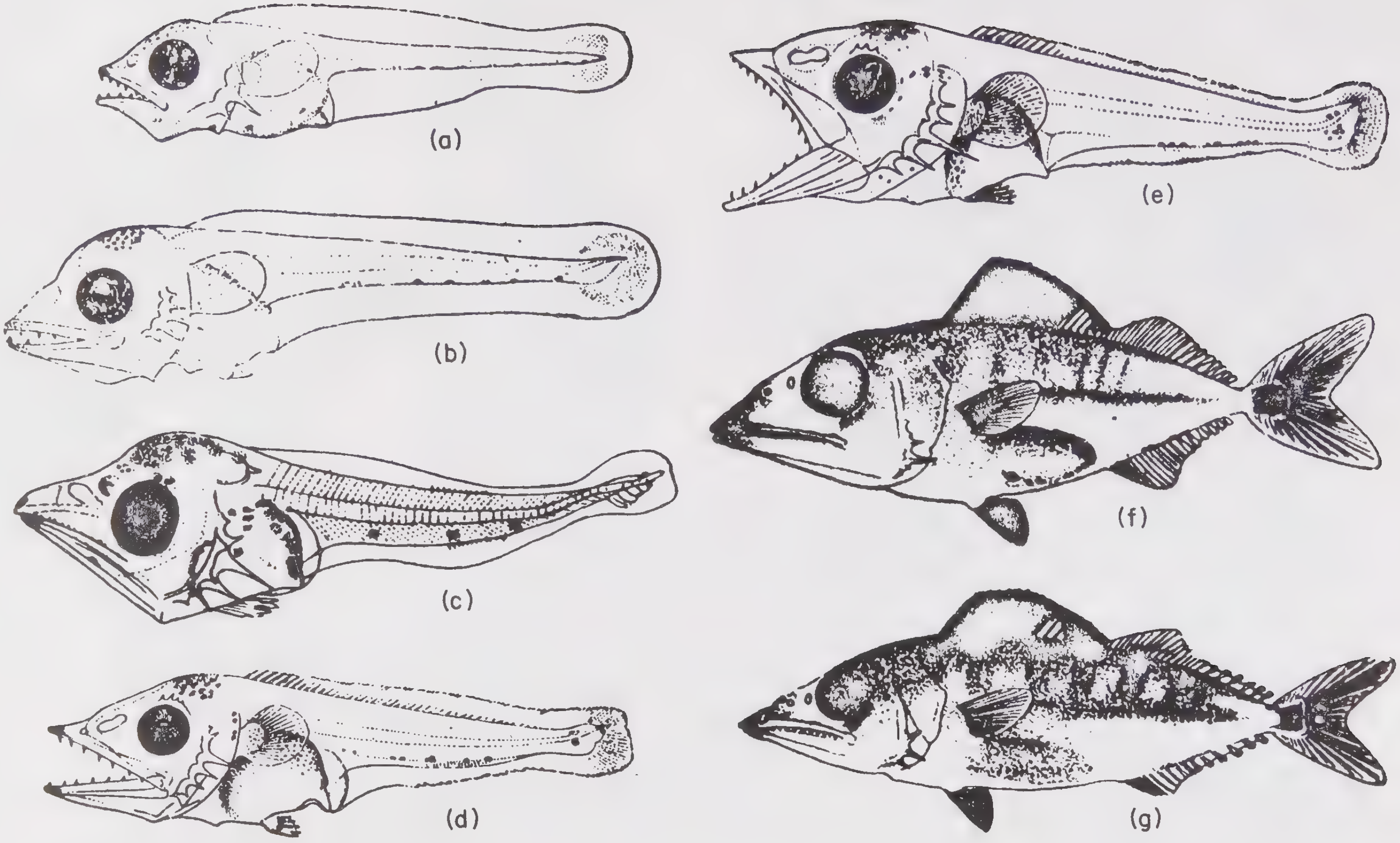

Figure 10.—The postlarvae of *Sarda sarda*: (a) 5.45 mm (from Vodianitskii and Kazanova 1954, fig. 12); (b) 6.98 mm (from Vodianitskii and Kazanova 1954, 1954, fig. 12); (c) 7.20 mm (from Ehrenbaum 1924); (d) 9.59 mm (from Vodianitskii and Kazanova 1954, fig. 12); (e) 11.00 mm (from Vodianitskii and Kazanova 1954, fig. 12); (f) 26.5 mm (from Buen 1932); (g) 32 mm (from Buen 1932).

insertion of the anal fin, 65%; there are about 20 segments in the postanal region.

In a 26.5 mm specimen, the preopercular spines are well-evident but small (Fig. 10f). The caudal fin is now forked; the pectoral and ventral fins are relatively small. The membrane that is continuous with the second dorsal and anal fins still unites the finlets. The first dorsal is covered with black pigments except for a clear space at the base of the 10th to the 13th rays; the other fins are transparent. Fine black pigments are on the snout, the nape, and the dorsal region of the trunk where six vertical bands, which extend from the dorsal edge to about the middle of the flanks, begin to appear. A dark horizontal line separates the pigmented dorsal portion from the ventral, unpigmented portion. In a 32 mm specimen the preopercular spines are smaller but still evident (Fig. 10g). The membrane still joins the finlets and the fin coloration is unchanged. The pigmentation on the head is increased and the six vertical bands are quite pronounced.

Illustrations of postlarval *S. sarda* given by Vodianitskii and Kazanova (1954) are also shown in Figure 10.

Pinkas (1961) and Klawe (1961b) gave descriptions of postlarval *S. chiliensis*, and Jones (1960), Gorbunova (1963), and Harada et al. (1974) described larval and postlarval *S. orientalis* (Figs. 11, 12).

Except for *S. chiliensis* and *S. orientalis* in the eastern Pacific, where there may be some overlap in the distribution of these two species, the problem of identifying and separating the larval and juvenile species within the genus does not occur because the species are allopatric. As for the larval forms of *S. chiliensis* and *S. orientalis* in the eastern Pacific, Klawe (1961b) stated that it would be impossible to separate the two species without a complete developmental series of both species. Klawe further noted that it should be possible to distinguish juvenile *S. chiliensis* and *S. orientalis* from each other based on gill raker counts even at a relatively small size. Pinkas (1961) pointed out other characters (number of teeth on lower jaw and presence or absence of posterior gill teeth) that could be used to separate *S. chiliensis* >24 mm from similar sized *S. velox* (= *S. orientalis*).

Once the juveniles acquire the full adult complement of certain characters, which seems to be at a relatively small size (Pinkas 1961; Klawe 1961b), the summary of distinguishing characters (Table 1) for the four species of *Sarda* compiled by Collette and Chao (1975) indicates that the juveniles should be separable without difficulty. *Sarda australis, S. chiliensis,* and *S. orientalis* can be separated from each other on the basis of gill raker counts while *S. sarda* can be distinguished from all the others by the number of vertebrae.

3.3 Adult phase

3.31 Longevity

See section 4.13.

3.32 Hardiness

See section 3.52.

3.33 Competitors

Sarda chiliensis

The relationships of *S. c. lineolata* with the other species occupying the same areas off southern California are not clear. However, recent changes in the species composition of pelagic fish stocks off California shores may involve the bonito as well as Pacific sardine, *Sardinops sagax,* and northern anchovies, *Engraulis mordax* (Frey 1971). Presumably these changes would involve the ability of the various species to compete with one another for food and space. Behavior studies on *S. c. lineolata* indicate that they can compete very well with other species in obtaining food. In a fish tank containing Pacific barracuda, *Sphyraena argentea;* yellowtail, *Seriola dorsalis;* and tarpon, *Megalops atlantica, S. c. lineolata* was the first species to reach and ingest food tossed onto the surface (Magnuson and Prescott 1966). Magnuson and Prescott noted that the high speed of *S. c. lineolata* gives it an advantage over the other species in a "scramble" type of competition.

Sarda orientalis

In the Indian Ocean adult *S. orientalis* are often caught together with *Euthynnus affinis, Auxis* spp., *Thunnus tonggol,* and *Scomberomorus* spp. and presumably compete with these species for food (Silas 1963). Demir (1963) stated that all predatory fishes and dolphins are potential competitors of *S. sarda,* including *Delphinus delphis ponticus, Tursiops truncatus, Scomber scombrus, Trachurus mediterraneus, Pomatomus saltatrix* in the Black Sea, and additionally, *Scomber japonicus, Auxis rochei,* and *Euthynnus alletteratus* in the Sea of Marmara.

3.35 Parasites, diseases, injuries, and abnormalities

Records of parasitism on bonitos include a trematode, *Didymozoon pelamyzis,* from the gill lamella of *S. sarda* from the Black Sea, Sea of Marmara, and the Mediterranean (Dawes 1946; Demir 1963). Larvae of the cestode *Callitetrarhynchus gracilis* have been found in the body cavity and the isopod *Livoneca* sp. from the gill lamellae of *S. sarda* (Postel 1954). Parasitic copepods *Caligus sarda* (Pearse 1952) and *Ceratocolax euthynni* (Vervoort 1971) have been found on *S. sarda.* Silas (1967) and Silas and Ummerkutty (1967) produced a detailed listing of the parasites of scombroid fishes, including *Sarda* (Table 13).

Two stripeless *S. c. lineolata* have been recorded from waters off La Jolla, Calif. (Matsumoto et al. 1969). These specimens possessed all the meristic characters typical of *S. c. lineolata* except that they lacked stripes.

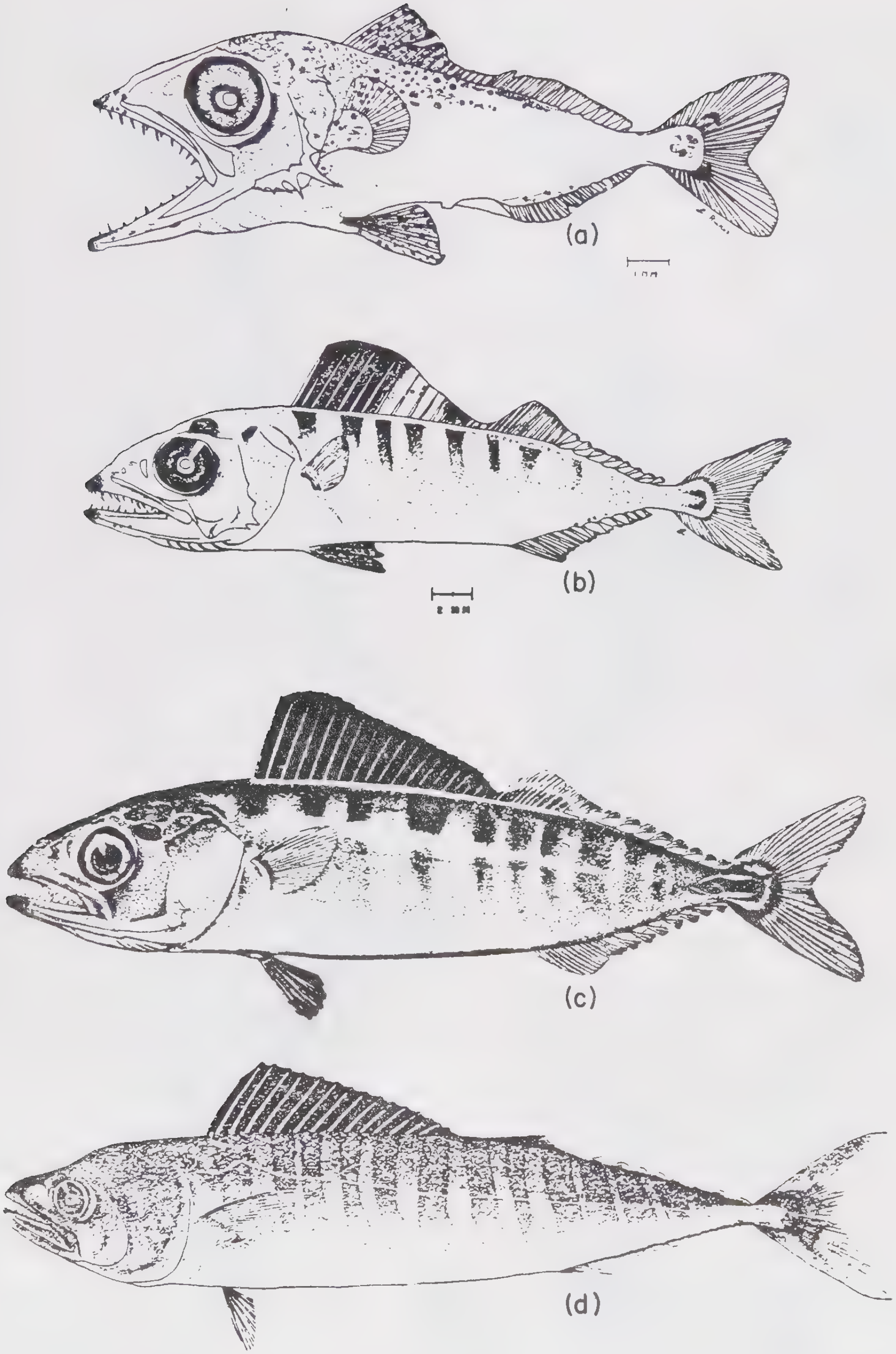

Figure 11.—Postlarval *Sarda chiliensis*: (a) 16.7 mm fork length (from Pinkas 1961, fig. 4); (b) 33.0 mm fork length (from Pinkas 1961, fig. 5); (c) 42 mm (from Klawe 1961b, fig. 3); (d) 160 mm (from Klawe 1961b, fig. 4).

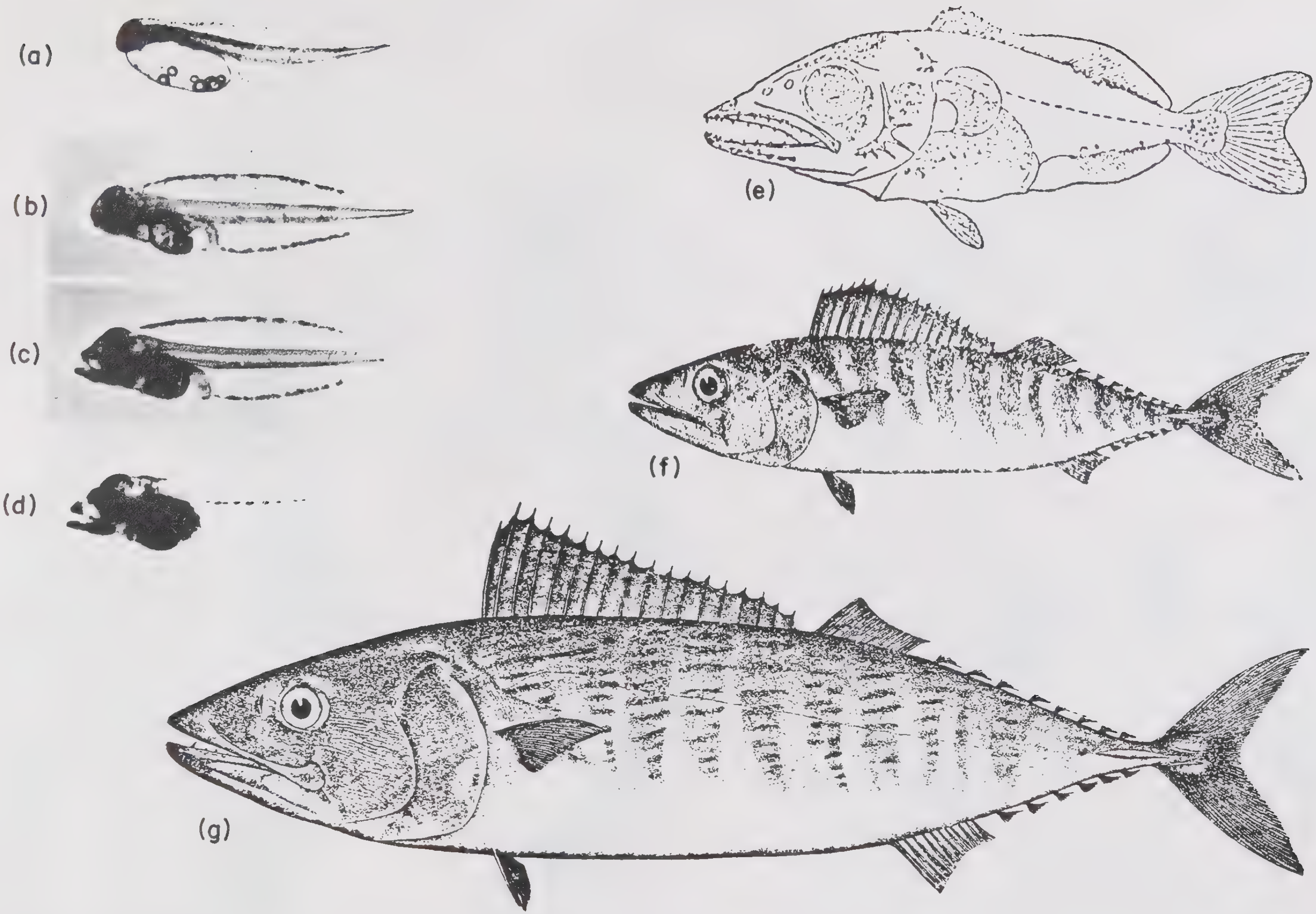

Figure 12.—Larval and postlarval *Sarda orientalis*: (a) 4.2-mm larva (from Harada et al. 1974, plate 1); (b) 2-day-old larva (from Harada et al. 1974, plate 1); (c) 5-day-old larva (from Harada et al. 1974, plate 1); (d) 8-day-old larva (from Harada et al. 1974, plate 1); (e) 11.56 mm larva (from Gorbunova 1963, fig. 12); (f) 80.0 mm postlarva (from Jones 1960, fig. 11); (g) 158.0 mm postlarva (from Jones 1960, fig. 10).

Table 13.—Parasites of *Sarda*. (Modified from Silas 1967; Silas and Ummerkutty 1967.)

Copepods	Monogenetic trematodes	Digenetic trematodes	Cestodes
		Sarda chiliensis	
Caligus bonito			
Caligus mutabilis			
Pseudocycnus appendiculatus			
		Sarda orientalis	
Caligus bonito	*Capsala caballerio*	*Bucephalopsis cybii*	
Caligus coryphaenae			
Caligus productus			
		Sarda sarda	
Caligus bonito	*Capsala pelamydis*	*Aponurus tschugunowi*	*Grillotia erinaceus*
Caligus mutabilis	*Hexostoma pricei*	*Atalostrophion sardae*	*Lacistorhynchus tenus*
Caligus pelamydis	*Hexostoma thynni*	*Bucephalopsis arcuata*	*Scolex pleuronectis*
Caligus productus		*Dinurus barbatus*	*Tentacularia bicolor*
		Hirudinella clavata	*Tentacularia coryphaena*
		Lecithochirum caudiporum	*Tetrarhynchus megabothrium*[1]
		Lecithochirum texanum	*Tetrarhynchus scomber-pelamys*[1-2]
		Nematobothrium pelamydis	*Tetrarhynchus sp.*[3]
		Opecoelides vitellosus	
		Rhipidocotyle angusticollis	
		Tormopsolus orientalis?	
		Unitubulotestes sardae	

[1] Species incertae sedis.
[2] Indicates doubtful record.
[3] Forms unidentifiable.

3.4 Nutrition and growth

3.41 Feeding

Magnuson and Heitz (1971) examined the relation between the gill raker morphology and the food habits of scombrid fishes, including *S. c. lineolata*. In the past, the high diversity of food organisms in the stomachs of scombrids gave rise to the opinion that scombrids are nonselective feeders. However, Magnuson and Heitz pointed out that selectivity does exist in terms of food size in scombrid food habits in that the stomach contents of small and large fish of the same species were dissimilar. They suggest that larger predators have a reduced ability to catch small prey (crustaceans) because of a relatively large gap between the gill rakers. Among scombrids of the same size *S. c. lineolata* and *S. orientalis* had the largest gill gaps (1.8-3.3 mm). The relative unimportance of crustaceans in the food habits of *S. c. lineolata* noted by Pinkas et al. (1971) could be related in part to the large gill gaps in this species. The data presented by Magnuson and Heitz (1971) also indicate a relationship between the number of gill rakers and the gill raker gap, i.e., the greater the number of gill rakers, the smaller the gill raker gap. *Sarda orientalis* have fewer gill rakers than *S. chiliensis* (Collette and Chao 1975), and as Magnuson and Heitz's data show, the gill raker gap is greater in *S. orientalis*. Therefore, it would be expected that the diet of S. c. lineolata would contain a larger proportion of smaller organisms than that of S. orientalis.

3.42 Food

Sarda australis

Only a few miscellaneous observations are available on the feeding habits of the Australian bonito. Particularly during the winter months, *S. australis* occurs commonly in schools in the inshore coastal waters of Queensland and feeds on hardyheads, *Pranesus ogilbyi;* pilchards, *Sardinops neopilchardus;* and anchovies, *Engraulis australis* (Grant 1972). Munro (1958) indicated that they also feed on mackerel scad, *Trachurus mccullochi*.

Sarda chiliensis

A detailed study of the food habits of *S. c. lineolata* was conducted by Pinkas et al. (1971) based on a total of 1,498 stomachs collected in 1968 and 1969 from fish captured in nearshore waters of southern California and Baja California. Their study clearly showed that the northern anchovy, *Engraulis mordax*, was the major food item in the diet of *S. c. lineolata*. The common squid, *Loligo opalescens*, ranked next in importance, and miscellaneous fishes and a few crustaceans made up the small remainder of the diet of *S. c. lineolata* (Table 14).

Table 14.—Food of *Sarda chiliensis lineolata*, 1968 and 1969. (From Pinkas et al. 1971.)

Food items	Number	Percent number	Volume (ml)	Percent volume	Frequency of occurrence	Percent frequency of occurrence
Fishes						
Engraulidae						
Engraulis mordax	4,159	75.5	11,356.4	75.9	462	56.3
Scomberesocidae						
Cololabis saira	27	0.5	190.8	1.3	16	1.9
Gadidae						
Merluccius productus	24	0.4	6.8	<0.1	15	1.8
Carangidae						
Trachurus symmetricus	16	0.3	185.6	1.2	13	1.6
Sciaenidae						
Genyonemus lineatus	1	<0.1	38.0	0.3	1	0.1+
Seriphus politus	3	+0.1	1.3	<0.1	2	0.2+
Embiotocidae						
Brachyistius frenatus	1	<0.1	10.0	<0.1	1	0.1+
Cymatogaster aggregata	1	<0.1	14.0	0.1	1	0.1+
Zalembius rosaceus	1	<0.1	9.0	<0.1	1	0.1+
Scorpaenidae						
Sebastodes spp.	12	0.2	5.8	<0.1	5	0.6
Stromateidae						
Peprilus simillimus	7	0.1+	195.0	1.3	6	0.7
Bothidae						
Citharichthys sordidus	1	<0.1	0.6	<0.1	1	0.1+
Unidentified fishes	765	13.9	223.8	1.5	185	22.5
Subtotal, fishes other than Engraulidae	859	15.6	880.7	5.9	247	30.1
Subtotal, all fishes	5,018	91.1	12,237.1	81.8	709	86.4
Cephalopods						
Loligo opalescens	448	8.1	2,690.7	18.0	207	25.1
Onychoteuthis boreali-japonicus	1	<0.1	3.7	0.2	1	0.1+
Unidentified cephalopods	17	0.3+	9.9		16	2.0
Crustaceans						
Pleuroncodes planipes	4	<0.1	5.6		4	0.5
Crab megalops larvae	3	<0.1	0.1		1	0.1+
Unidentified animals	19	0.3+	4.7		17	2.0
Subtotal, all invertebrates (except *Loligo opalescens*) and unidentified animals	44	0.8	24.0	0.2	39	4.8
Totals	5,510	100.0	14,951.8	100.0	—	—

There was a seasonal variation in the importance of the common squid in the diet of *S. c. lineolata*. Squid was most important in the first and second quarters of the year but was less important in the third quarter of the year. This seasonal pattern of the importance of squid in the bonito's diet was related to the seasonal concentrating behavior of squid during its reproductive cycle.

Sarda orientalis

Information on the food and feeding habits of *S. orientalis* in Japanese waters is fragmentary. Yabe et al. (1953) examined 18 stomachs from juvenile *S. orientalis* in southern Kyushu waters. Fifteen of the 18 stomachs were empty, 2 of the stomachs contained *Engraulis japonicus* remains, and 1 stomach contained unidentifiable fish remains. Yokota et al. (1961) examined stomachs of 24 *S. orientalis* caught in about the same area and found a total of five saury, one *Sphyraena* sp., one squid, and one carangid in the stomachs.

Kumaran (1964) investigated the food habits of *S. orientalis* in the Indian Ocean based on 43 specimens ranging in length from 85 to 305 mm. The most important single food item was *Anchoviella commersonii*. Fishes of lesser importance in the diet were *Leiognathus insidiator*, *Decapterus russelli*, and *Sardinella* sp. Kumaran noted that the variety of food organisms was smaller in the stomachs of *S. orientalis* as compared with *Euthynnus affinis* and *Auxis*. He gave as the reason for this the fact that all the *S. orientalis* specimens were collected from a single locality. Sivasubramaniam (1969) looked at the food-bearing stomachs of 11 *S. orientalis* caught in the waters around Sri Lanka. Nearly 60% by volume of the food consisted of a clupeoid fish, 18% cephalopod mollusk (squid and octopus), 15% decapod crustacea, and 7% miscellaneous items including unidentified fishes.

Sarda sarda

More information is available on the food and feeding habits of *S. sarda*, including information on larval and juvenile stages. Larval *S. sarda* about 5 mm long start active feeding even before the yolk sac is completely absorbed. Larvae >6-7 mm feed on relatively large organisms, including fish larvae, but prefer copepods. Juveniles >18-20 mm feed on the larvae of anchovy, horse mackerel, and *S. sarda* (Mayorova and Tkacheva 1959). Zusser (1954) reported a *Pseudocalanus* in the stomach of a 7.2 cm juvenile and a 4.5 cm long anchovy in a 8.7 cm juvenile. Demir (1963) found a single 3.5 cm horse mackerel from the stomachs of 44 juvenile *S. sarda* ranging in length from 6.5 to 16 cm taken in the Black Sea, the Sea of Marmara, and the Bosporus from 1957 to 1959. Because of the preponderance of empty stomachs, Demir believes that the juveniles, like the adults, regurgitate their food at the moment of capture.

Demir (1963) stated that adult *S. sarda* is an insatiable predator that feeds diurnally. Feeding in Turkish waters is much more vigorous in the early morning and towards evening. Demir noted that the feeding season is usually from the second half of April to the end of October in Turkish waters. *Sarda sarda* adults primarily feed on smaller schooling fishes, the species depending on the locality (Table 15).

In the western Atlantic in the Gulf of Maine, *S. sarda* prey on mackerel, alewives, menhaden, other small fishes such as launce and silverside, and squid (Bigelow and Schroeder 1953). Boschung (1966) examined the stomachs of 52 *S. sarda* taken during a fishing tournament in the Gulf of Mexico and noted that the fish had fed on a variety of fishes and invertebrates. They included: a clupeid (probably *Harengula pensacolae*); harvestfish, *Peprilus paru*; spot, *Leiostomus xanthurus*; anchovies, *Anchoa* sp.; mackerel, *Scomberomorus* sp.; sea robin, *Prionotus* sp.; squid, *Loligo* sp.; shrimp, *Penaeus* sp.; and unidentified fishes.

Table 15.—Food of *Sarda sarda* in the Black Sea, Sea of Marmara, and the eastern Atlantic. (From Berg et al. 1949; Postel 1954; Zusser 1954; Slastenenko 1956; Ionescu et al. 1958; Demir 1963.).

Black Sea

Engraulis encrasicholus
Spratella sprattus phalerica
Ammodytes cicerellus
Scomber scombrus
Trachurus mediterraneus
Mullus barbatus
Pomatomus saltatrix (young)
Sarda sarda (young)
Mugil spp.
Atherina spp.
Gobiidae

Sea of Marmara

Important food items
- *Engraulis encrasicholus*
- *Spratella sprattus phalerica*
- *Scomber scombrus*
- *Scomber colias*
- *Clupea pilchardus*
- *Ammodytes cicerellus*
- *Trachurus mediterraneus*

Less important food items
- *Smaris alceda*
- *Trachurus trachurus*
- *Boops boops*
- *Mullus barbatus*
- *Atherina* spp.

Atlantic Ocean near Dakar, Senegal

Sardinella sp.
Engraulis sp.
Scomber colias
Ammodytes sp.
Planktonic crustaceans
- Caprella
- Euphausiid spp.

Sarda sarda can swallow relatively large prey and the adults and juveniles are both cannibalistic. There is a record of a 38 cm *S. sarda* from the stomach of a 63 cm fish (Zusser 1954).

3.43 Growth rate

Sarda australis

There is almost nothing in the literature on the age and growth of *S. australis* except that they grow to 91.4 cm (36 in) (Ogilby 1954).

Sarda chiliensis

In the waters between southern California and northern Baja California *S. c. lineolata* spawns between January and May and the pelagic fertilized eggs take about 3 days to hatch. Young *S. c. lineolata* are first observed in the early summer when they are 15.7-25.4 cm (6-10 in) and by the following spring they are about 38.1 cm (15 in) long and weigh from 0.7 to 0.9 kg (1.5 to 2 lb). In the fall these fish may weigh 1.4 kg (3 lb) or more and by the following year in May, they may weigh 2.7-3.2 kg (6-7 lb). When they are 4 yr old, they are 71.1 cm (28 in) and weigh about 5.4 kg (12 lb) (Frey 1971). These data are probably the result of random observations and not a systematic study.

Kuo (1970) made a detailed study of the growth of *S. chiliensis* from southern California waters and from Peru based on otoliths (Fig. 13). Kuo fitted the von Bertalanffy growth function to his data and found that the length-at-age of bonito from the two areas did not differ for age 1, 2, and 6 fish but that there was a significant difference in size of fish 3-5 yr old (Table 16). The growth equations obtained for the northern and southern populations, respectively, were:

$$L_t = 2{,}661\,[1 - e^{-0.038(t + 0.60)}]$$

and

$$L_t = 1{,}014\,[1 - e^{-0.154(t + 0.015)}],$$

where L_t is fork length in millimeters and t is actual age in years.

Campbell and Collins (1975) also determined the age and growth of the northern population of *S. chiliensis* based on a sample of 3,139 fish ranging in length from 23 to 79 cm landed at the canneries in San Pedro, Calif. These fish were caught in an area between central Baja California and Point Conception, Calif., from 1968 to 1974. Like Kuo (1970), Campbell and Collins used otoliths to age the fish and used the von Bertalanffy growth function to describe the growth as shown below:

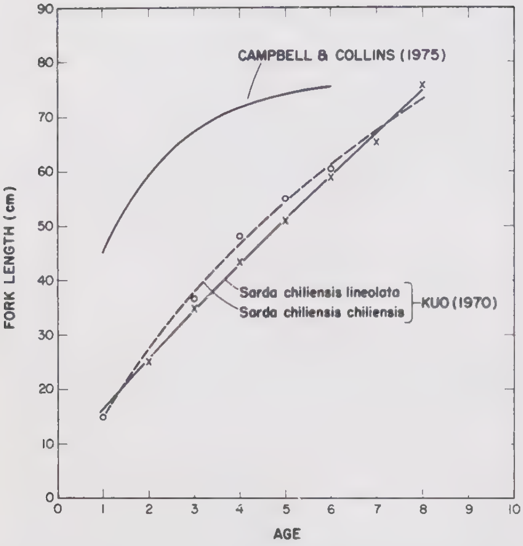

Figure 13.—Growth of *Sarda chiliensis* from southern California and Peru. (Note: The abscissa of the Campbell and Collins curve is age class.) (From Kuo 1970; Campbell and Collins 1975, fig. 4.)

Table 16.—Age-length data for the subspecies of *Sarda chiliensis*. (From Kuo 1970, table 14.)

Age	Species[1]	Mean length (mm)	Standard error	Confidence interval (mm)	*N*
1	*lineolata*	152	0.95	150-154	222
	chiliensis	151	1.99	147-155	141
2	*lineolata*	252	1.28	249-254	219
	chiliensis	256	2.76	250-261	137
3	*lineolata*	347	1.70	344-351	212
	chiliensis	364	6.02	352-376	43
4	*lineolata*	433	2.26	429-438	182
	chiliensis	480	7.01	466-494	26
5	*lineolata*	509	3.19	503-515	133
	chiliensis	550	7.27	535-565	25
6	*lineolata*	585	4.79	576-595	74
	chiliensis	604	9.18	585-623	24
7	*lineolata*	652	13.00	625-678	35
	chiliensis	—	—	—	0
8	*lineolata*	756	12.10	728-783	9
	chiliensis	—	—	--	0

[1] *lineolata* = *Sarda chiliensis lineolata.* [Northern Hemisphere]
chiliensis = *Sarda chiliensis chiliensis.* [Southern Hemisphere]

$$L_t = 76.87\,[1 - e^{-0.6215(t+0.410)}],$$

where L_t is fork length in centimeters and t is age at capture, which is about 0.375 yr (September) older than the given age.

The length-age relationship predicted by the curve for fish taken in the fishery is shown below:

Age	*Fork length (cm)*
1	44.9
2	59.7
3	67.6
4	71.9
5	74.2
6	75.4

The growth curve is also shown in Figure 13.

The maximum size of *S. chiliensis* in the Northern Hemisphere is about 101.6 cm (40 in) and about 11.3 kg (25 lb). There is an unverified record of a 16.8 kg (37 lb) specimen, but bonito over 11.3 kg are rare (Frey 1971). In light of these observations, the L_∞ of 2,661 mm obtained by Kuo (1970) for the Northern Hemisphere bonito seems unreasonably large. On the other hand, as noted by Campbell and Collins (1975), the L_∞ predicted by the von Bertalanffy growth function as fitted to their data was less than what they had observed in the California fishery and much less than the maximum length of *S. chiliensis* (101.6 cm) in the literature. They noted that the discrepancy could have been caused by the lack of fish larger than 79 cm in their sample.

It is of interest also that the growth curves obtained by Kuo (1970) and Campbell and Collins (1975) for the northern population of *S. chiliensis* are quite different. The results obtained by Campbell and Collins indicate a rapid growth rate during the first 3 yr and a tapering off to a relatively low rate thereafter. Kuo's growth curve on the other hand shows only a slight curvature and suggests almost linear growth for the northern bonito population (Fig. 13). The age-length data given by Campbell and Collins (1975) and Kuo (1970) are also quite different. The lengths at the different ages as given by Campbell and Collins are larger for all the ages than those given by Kuo.

The maximum size of *S. chiliensis* in the Southern Hemisphere is not well defined. Barrett (1971) sampled the fish landed in the Chilean fishery and noted that the maximum size of fish landed was 74 cm. In an earlier study Buen (1958) found fish as large as 79 cm. Mann (1954) stated that Chilean bonito grows larger than 80 cm.

Sarda orientalis

Very little information is available on the age and growth of *S. orientalis*. Yabe et al. (1953) presented data on the mean lengths of six samples of *S. orientalis* ranging in length from 161 to 348 mm that were sampled at Aburatsu, Japan, over an irregular period from 26 August to 17 October 1950 (Table 17). The mean lengths of fish from the six samples were plotted against sampling date, and a straight line was drawn by eye through the data points (Fig. 14). If the line is a reasonable representation of the growth of *S. orientalis* between 161 and 348 mm, it indicates a mean growth of about 2.6 mm/day. Harada et al. (1974) made observations on the growth of larval and juvenile *S. orientalis* in artificial fertilization experiments. They determined that the fertilized eggs hatched in about 50 h in water temperature ranging from 20° to 24°C and that the newly hatched larvae were 4.1-4.3 mm in total length. The larvae grew to 14 mm in total length

Table 17.—Lengths of *Sarda orientalis* landed at Aburatsu, Japan in 1950. (From Yabe et al. 1953, table 11.)

Date	No. of fish	Body length (mm)	
		Range	Mean
Aug. 26	17	205-221	214
Sept. 1	2	241-249	245
Sept. 2	3	233-243	239
Sept. 8	5	161-270	239
Sept. 9	10	254-277	263
Oct. 17	5	333-348	339

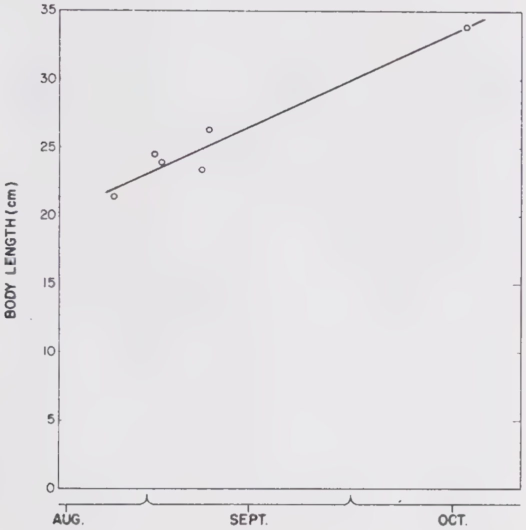

Figure 14.—Growth of juvenile *Sarda orientalis* in Japanese waters. (Data from Yabe et al. 1953.)

in 10 days, to 74 mm in 20 days, to 106 mm in 30 days, to 219 mm in 42 days, and to 290 mm in 99 days after hatching. This growth rate represented the fastest growth under the conditions provided in the experiment. The growth rate of larval and juvenile *S. orientalis* indicated by these experiments was about 2.9 mm/day during the 99-day period and compares favorably with that suggested by the data presented by Yabe et al. (1953). Harada et al. (1973) presented some data on the growth of *S. orientalis* kept in artificial enclosures. Thirty-three *S. orientalis* 40 cm long and 675 g in weight grew to 50 cm and 1,500 g in about 4 mo.

Regarding the maximum size of *S. orientalis* in the Indian Ocean, the large specimens off the southwest coast of India are generally less than 70 mm long (Silas 1964). Smith (1949) stated, however, that *S. chiliensis* (= *S. orientalis*) grows to at least 101.6 cm (40 in). In Japanese waters *S. orientalis* grows to about 80 cm and 1.5-3.0 kg (Kishinouye 1923).

Sarda sarda

Various investigators have presented monthly length data for young *S. sarda* from the Black Sea (Table 18).

Table 18.—Monthly length data for *Sarda sarda* from the Black Sea. (Data from Demir 1963.) (Note: The author did not define the length dimension.)

Author	July	Aug.	Sept.	Oct.
	Length (cm)			
Zusser (1954)	—	19-27	27-29.5	25-36
Tkacheva (1958)	—	21-33	27-36	36-40
Mayorova and Tkacheva (1959)	—	21-33	27-37	36-41
Demir (1963)	6-16	12-32	25-38	33-42

The data were given as the ranges of lengths sampled during monthly periods, and the midpoints of the length ranges were plotted to represent the growth of 3-42 cm *S. sarda* in the Black Sea (Fig. 15). As would be expected, there is some variation in the data presented by the various investigators, but the variation was relatively small. In gross terms these data suggest that *S. sarda* grew about 252 mm in 90 days (7.5-11 cm in July to 30.5-38.5 cm in October) or at a growth rate of 2.8 cm/day.

Demir (1963) summarized the age-length relation of *S. sarda* determined by various authors (Table 19). Subsequent to the publication of Demir's paper, Kutaygil (1967) published some data on age-length determinations on *S. sarda* (Table 20). Kutaygil used otoliths to age the fish and also back-calculated the lengths of the fish at various ages. He noted that bonito from different year classes had different growth rates.

Zusser (1954), in contrast to the other investigators, gave age-length relations for fish up to 9 yr of age. Demir (1963), however, remarked that the age-length relations given by Zusser were probably erroneous. Although several age-length relations for *S. sarda* are available, as far as it is known, no one has tried to fit a growth curve to these data.

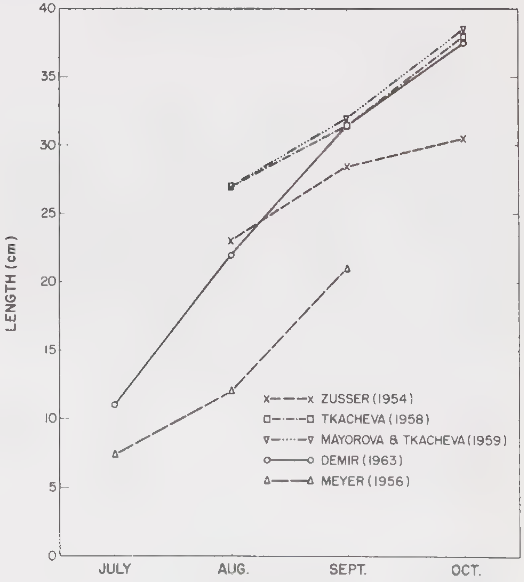

Figure 15.—Growth of juvenile *Sarda sarda* in the Black Sea.

Table 19.—Age-length relation in *Sarda sarda*. (From Demir 1963, table 4.) (Note: The length dimension was not defined by the author.)

Author	Age 1	2	3	4	5	6	7	8	9
	Length (cm)								
Zusser (1954)	25-37	33-50	42-54	50-62	56-67	60-70	63-76	70-78	74-85
	31.5	41.5	48.8	56.2	61.2	66.5	69.5	73.5	76.2
Nümann (1955)	38-41	53-57	60-64	—	—	—	—	—	—
Nikolskii (1957)	35.3	55.1	64.2	72.5	—	—	—	—	—
Türgan (1958)	30-40	50-55	55-60	60-65	—	—	—	—	—
Nikolov (1960)	38.85	52.6	60	67	(74-75)	—	—	—	—

Table 20.—Calculated lengths for each age of *Sarda sarda*. (From Kutaygil 1967, table 26.) (Note: The author did not define the length dimension.)

Sample			No. of fish	Age 1	2	3	4
1957	II	(1955)	7	44.0	59.1	—	—
	III	(1954)	22	45.4	57.9	64.8	—
	IV	(1953)	4	47.6	59.2	64.5	68.7
	Grand mean =			45.1	58.3	64.9	
	N =			33	33	26	
Jan. 1958	IV	(1954)	5	42.9	53.3	60.6	64.2
Feb. 1958	IV	(1954)	18	41.1	52.9	59.2	63.8

The largest *S. sarda* is about 85 cm in the Black Sea. Of *S. sarda* in the western Atlantic, Bigelow and Schroeder (1953) stated that they grow to about 91.4 cm (36 in) and 4.5-5.4 kg (10-12 lb). Hammond and Cupka (1975) noted that *S. sarda* seldom exceeds 6.8 kg (15 lb).

3.5 Behavior

3.51 Migrations and local movements

See also section 5.3.

The seasonal migrations of *S. sarda* from the Aegean Sea through the Sea of Marmara to the Black Sea have been well documented. The migration routes were presumably determined by the development of the fisheries in these areas and were verified by tagging experiments (Demir 1963). The migration from the Aegean Sea to the Black Sea starts toward the end of April and lasts to the beginning of June or later. The return migration from the Black Sea to the Aegean Sea usually starts in September and lasts to the end of November. Some of the bonito schools returning from the Black Sea may stay in the Sea of Marmara but others continue on to the Aegean Sea.

The *S. sarda* in the Adriatic Sea apparently make a north-south migration within that sea down to around the Greek islands (Belloc 1954). The bonitos leave the upper Adriatic in November-December and travel along both shores of the Adriatic, arriving in Greek waters in February-March. The return migration starts around August. In addition, there apparently are schools of bonito that remain the whole year round in Greek waters and in waters along the east coast of Sicily.

The relation of the bonitos in the Aegean Sea-Sea of Marmara-Black Sea complex with the Adriatic Sea bonito and with the bonitos in the other parts of the Mediterranean is not clear. Turkish investigators imply that the stock in the Aegean Sea-Sea of Marmara-Black Sea complex originates in the Aegean Sea and the Sea of Marmara (Demir 1957) and remain within this complex.

In the eastern Pacific, over 11,200 *S. c. lineolata* have been tagged and released since 1968 along the coast from Monterey Bay, Calif., to Cape San Lazaro, Baja California (Collins and MacCall 1977). Recoveries of tagged fish have indicated that they move randomly in local California waters, although there was a definite movement down the southern California coast in the winter and a northward movement in the late summer and fall, apparently in response to changes in sea temperature. Their tagging study also indicated that heated water discharges from coastal electric generating stations strongly influence the migration of young *S. c. lineolata.* Fish tagged in heated water plumes either remained in the area of the discharge or tended to migrate to another heated discharge area.

3.52 Schooling

All species of *Sarda* generally appear to be schooling fish. *Sarda australis* commonly occur in schools in inshore coastal waters of Queensland, Australia (Grant 1972). Frey (1971) stated that the *S. chiliensis* of the Northern Hemisphere is a pelagic schooling fish. Tominaga (1943), however, observed that *S. orientalis* in Japanese waters do not aggregate densely, rarely come to the surface of the sea, and always swim around reefs or near a cape where the current is strong, and that they never go out to the high seas. Conflicting observations are available on schooling of *S. orientalis* in the Indian Ocean. Silas (1963) stated that schools of adults and young appear along the southwest coast of India. Sivasubramaniam (1969), however, noted that *S. orientalis* are very seldom seen in surface schools of mixed tunas and when they are caught from mixed schools, the catch never exceeds six fish. All of the observations on *S. sarda* indicate it is a schooling fish. Demir (1963) stated that *S. sarda* gathers in dense schools of many thousands of fish of about the same size. *Sarda sarda* in the western Atlantic is a schooling fish, traveling in large aggregations. It is usually found at the surface, although occasionally it is caught near the bottom (Idyll and de

Sylva 1963). Of *S. sarda* that occurs in the Gulf of Maine, Bigelow and Schroeder (1953) wrote, "The bonito is a strong, swift, predaceous inhabitant of the open sea and like its tribe travels in schools."

3.53 Responses to stimuli

A detailed, systematic study on the behavior of captive *S. c. lineolata* in a large fish tank at Marineland of the Pacific, Palos Verdes, Calif., was made by Magnuson and Prescott (1966). The courtship and spawning behavior of *S. c. lineolata,* as reported by Magnuson and Prescott, was discussed earlier in sections 3.11 and 3.13. Further results of their observations are detailed below.

About 25 *S. c. lineolata* out of 60 that were caught near Marineland of the Pacific became established in the tank and were used in the observational program. Of the 25 survivors, 10 fish lived for 38 mo in captivity. The tank used was part of a public display and contained more than 800 other fishes of over 40 species. Part of the daily routine included five 15-min shows in which a diver entered the tank to feed the fish. Magnuson and Prescott noted that the *S. c. lineolata* "appeared habituated to show announcements and background music as well as to sounds made by tapping on the tank windows and sides." These observations indicate that *S. c. lineolata* are able to adapt to various environmental conditions.

In the Marineland of the Pacific tank, *S. c. lineolata* swam continuously against the current averaging 88.2 cm/s at a tail-beat frequency of 1.42 beats/s when not feeding or courting. *Sarda c. lineolata* apparently are less powerful swimmers than skipjack and yellowfin tunas. In fish about the same length (bonito, 57 cm; skipjack tuna, 57 cm; yellowfin tuna, 52 cm) Magnuson and Prescott noted that at four tail beats/s *S. c. lineolata* traveled only 170 cm/s whereas *Katsuwonus pelamis* averaged 230 cm/s and *T. albacares* averaged 240 cm/s.

Magnuson and Prescott observed nine miscellaneous behavior patterns in *S. c. lineolata*: mouth closure (long), mouth closure (short), snap, yawn, quick swim, lean, bend, jerk, and defecation. They discussed in detail the possible functions of all these miscellaneous behavior patterns. They hypothesized that mouth closure (long) movements could have been associated with olfaction or gill ventilation; snaps following a yawn or a quick swim with a drinking movement; leans may have a function as a social releaser in schooling; and bends and jerks may be associated with food passing through the alimentary canal.

No such detailed behavioral observations have been made on other species of *Sarda.* Inoue et al. (1967) were able to maintain *S. orientalis* up to 438 h in a pool. Inoue et al. (1970) determined that *S. orientalis* was negatively phototactic to both sunlight and artificial light. The swimming speeds of the fish (size not given) ranged from 0.3 to 0.56 m/s.

Table 21.—Sex ratio of *Sarda sarda* landed in Spain. (From Rodríguez-Roda 1966.)

Year	Month	Port	Males	Females	Ratio (Male:Female)
1963	June	Tarifa	17	18	1:1.06
1964	May	Barbate	57	20	1:0.35
1964	June	Barbate	25	24	1:0.96
1964	July	Barbate	18	24	1:1.33

4 POPULATION

4.1 Structure

4.11 Sex ratio

Sarda australis

No information.

Sarda chiliensis

Kuo (1970) obtained sex ratio data on *S. c. lineolata* that were caught from San Diego waters during a 1-yr period between 1964 and 1968. The percentage of females in the monthly samples varied from 37.5 to 70.3% and averaged 49.9% for the year. He found that the monthly sex ratios did not differ significantly from 1:1 except for the sample from the month of May.

The percentage of female *S. c. chiliensis* from eight samples of 100 bonito each obtained from the commercial catch landed at Iquique, Chile, varied from 47 to 65% between September 1968 and October 1969 (Barrett 1971). Barrett noted that more females were present in the catch during September-October spawning season, but stated that more data were needed to verify this observation.

Sarda orientalis

No information.

Sarda sarda

Rodríguez-Roda (1966) determined the sex ratio of four samples of *S. sarda* landed at the ports of Barbate and Tarifa, Spain (Table 21), in 1963 and 1964. The females in the samples ranged from 26 to 57.1%. Postel (1955b) presented data on the monthly sex ratio of *S. sarda* from the eastern tropical Atlantic (Table 22). In the Gulf of Mexico a sample of 52 *S. sarda* was composed of 31 males and 21 females (Boschung 1966).

4.12 Age composition

See section 4.13.

4.13 Size composition

Sarda australis

There is no information on the size or age of the fish except for generalized observations. The species grows to

Table 22.—Sex ratio of *Sarda sarda* from the eastern tropical Atlantic. (From Postel 1955b.)

Month	Males	Females	Ratio (Male:Female)
January	13	12	1:0.42
February	38	30	1:0.79
March	65	70	1:1.08
April	142	115	1:0.81
May	148	172	1:1.16
June	1	1	1:1
July	—	—	—
August	—	—	—
September	—	—	—
October	3	8	1:2.67
November	7	5	1:0:71
December	5	6	1:1.20
Total	422	419	1:0.99

about 90 cm (3 ft) but the average size of fish caught is about 40 or 45 cm (16 or 18 in) (Marshall 1964). Grant (1972) stated that the usual size taken is 1.8-2.3 kg (4-5 lb).

Sarda chiliensis

The length-frequency distribution of *S. c. lineolata* caught by sports fishermen from southern California waters shown in Figure 16 was prepared from data provided by C. M. Kuo[4] and is based on part of the *S. c. lineolata* sample he used in his study (Kuo 1970). Kuo measured 929 *S. c. lineolata* from southern California waters ranging in length from 331 to 750 mm. Both the male and female length-frequency distributions were similar: a single prominent mode was present between 510 and 540 mm.

MacCall et al. (1976) presented *S. c. lineolata* length-frequency data for the California commercial and party-boat fisheries in 1973 (Fig. 17). They stated that various segments of the fishery exploit different parts of the bonito population, which indicates an uneven geographical distribution of various age groups. It was indicated that, generally, the older fish were more available near Mexico and in offshore waters, although large fish were also taken in the fall off Santa Barbara. The party-boat fishery caught bonito <60 cm but the long-range party boats fishing off Mexico took older fish. The commercial fishery took larger fish. It is of interest that the modal size taken by the party boats during the period 1964-68 was larger than that taken in 1973. Recruitment strength is highly variable in southern California waters, and because the party-boat fishery takes only young fish, the catch per effort and the size composition of the catch reflect this variability and may account for the difference in modal sizes (MacCall[5]).

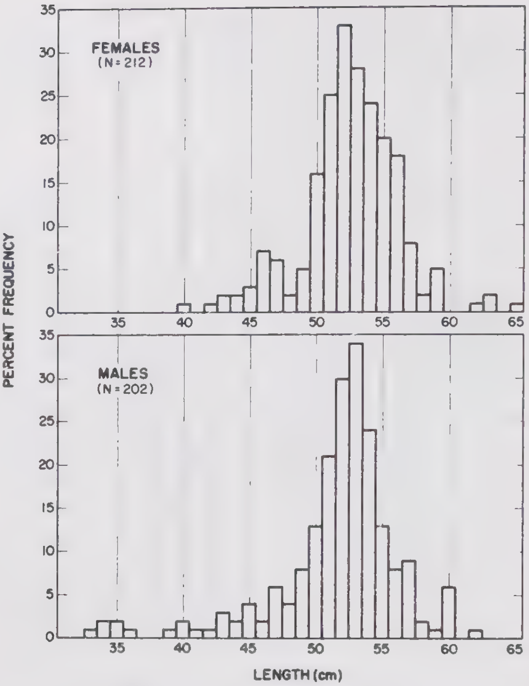

Figure 16.—Length-frequency distribution of *Sarda chiliensis lineolata* captured in the sport fishery in southern California.

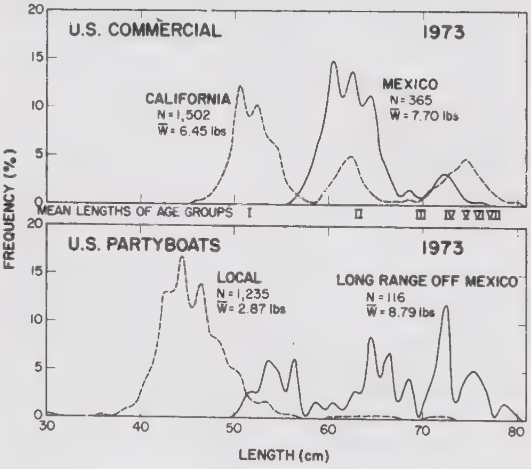

Figure 17.—Length-frequency distribution of *Sarda chiliensis lineolata* taken by the California commercial party-boat fisheries. (From MacCall et al. 1976, fig. 9.)

Barrett (1971) presented bonito length-frequency data from Chilean landings and noted that the larger bonito, in about the 62 cm modal group, made up most of the catch in September-October 1968 (Fig. 18). Most of the bonito in the April, August, September, and October 1969 landings, however, were smaller, 48-52 cm, and the larger fish were present only in July and August. Barrett

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[4] Presently with Oceanic Institute, Makapuu Point, Waimanalo, HI 96795.

[5] MacCall, A. D., California Department of Fish and Game, c/o National Marine Fisheries Service, La Jolla, CA 92038, pers. commun. February 1978.

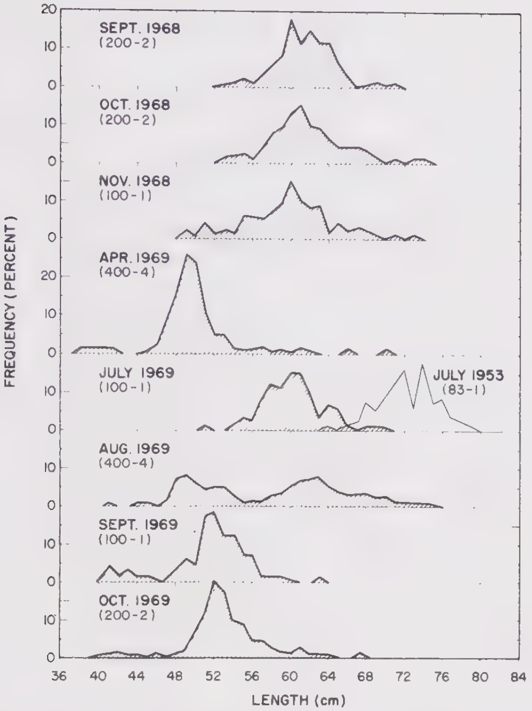

Figure 18.—Length-frequency distribution of *Sarda chilienss chiliensis* sampled from the commercial landings at Iquique, Chile, September 1968 to October 1969. Numerals in upper left corner of each panel indicate the month and year, number of fish, and number of samples. Unshaded distribution is from Buen (1958). (From Barrett 1971, fig. 4.)

further noted that the preponderant 72-74 cm modal group in 1953 reported by Buen (1958) was almost absent in the 1968 and 1969 samples, which indicated that the older fish were no longer present in the fishery in 1968 and 1969.

Vildoso (1962) and Barrett (1971) determined length-weight relationships for the southern *S. chiliensis* population and Campbell and Collins (1975) for the northern population (Table 23). In computing length-weight relationships, many investigators use a logarithmic transformation to linearize the data. Beauchamp and Olson (1973) pointed out that a bias is inherent in this procedure because the largest values are compressed on the logarithmic scale and provided a procedure to correct for this bias. As they pointed out, corrections for this bias have been outlined in the past but seldom used in practice and it is most likely that the length-weight relationships in Table 23 have not been corrected for bias.

Sarda orientalis

Sivasubramaniam (1969) presented length data for *S. orientalis* from the Sri Lanka fishery (Fig. 19). The average size of adult *S. orientalis* taken off southwest India was about 45 cm (Silas 1963).

Data on the size composition of the stock of *S. orientalis* in Japanese waters are almost nonexistent. Yabe et al. (1953) presented measurement data on a small sample of *S. orientalis* landed at Aburatsu, Japan (Table 17).

Sivasubramaniam (1966) determined the length-weight relationship for *S. orientalis* from the waters around Sri Lanka in the Indian Ocean (Table 23). The length-weight relationship is based on a sample of 25 fish, and although Sivasubramaniam did not give the size range of the fish, his figure 14 indicates that the fish ranged from about 24 to 51 cm.

Sarda sarda

Black Sea landings of *S. sarda* in the spring of 1955 were dominated by a group of fish centered at a length of 45 cm (Fig. 20). In the spring of the subsequent 2 yr, the same group of fish (1956, 55 cm; 1957, 60 cm; 1958, 65 cm) dominated the catch. This group of fish was the result of a strong year-class that originated in 1954 (Mayorova and Tkacheva 1959). Artuz (1959) also noted the same phenomenon. He sampled the landings at the Istanbul fish market and found that 3-yr-old fish (1954

Table 23.—Predictive length-weight relationships, $W = aL_b$, of *Sarda*. (Note: Various length and weight units were used in the original regressions, shown in the table. For ease in comparison, the constants were converted where needed so that the regressions are in terms of weight in grams and length in centimeters.)

			Size range of fish				
Species	Sex	No. of fish	Weight (g)	Length (cm)	*a*	*b*	Source
S. c. chiliensis	—	595	—	40-73	0.0118	3.02	Barrett (1971)
S. orientalis	—	25	—		0.0152	2.958	Sivasubramaniam (1966)
S. sarda	—	165	—	40-55.5	0.0149	2.971925	Rodríguez-Roda (1966)
S. c. lineolata	M	2,824	200-7,675	29-77	0.009088	3.09749	Campbell and Collins (1975)
S. c. lineolata	F				0.009611	3.08338	Campbell and Collins (1975)
S. c. lineolata	Sexes combined				0.009376	3.08962	Campbell and Collins (1975)
S. c. chiliensis	M	565	—	—	0.006491	3.19	Vildoso (1962)
S. c. chiliensis	F	513	—	—	0.006311	3.19	Vildoso (1962)

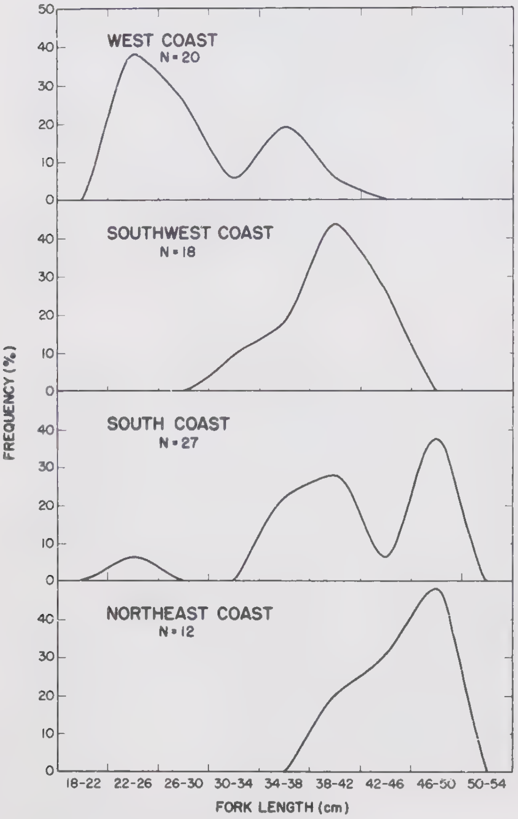

Figure 19.—Length-frequency distribution of *Sarda orientalis* around Sri Lanka (Ceylon) (1967-68). (From Sivasubramaniam 1969, fig. 1.)

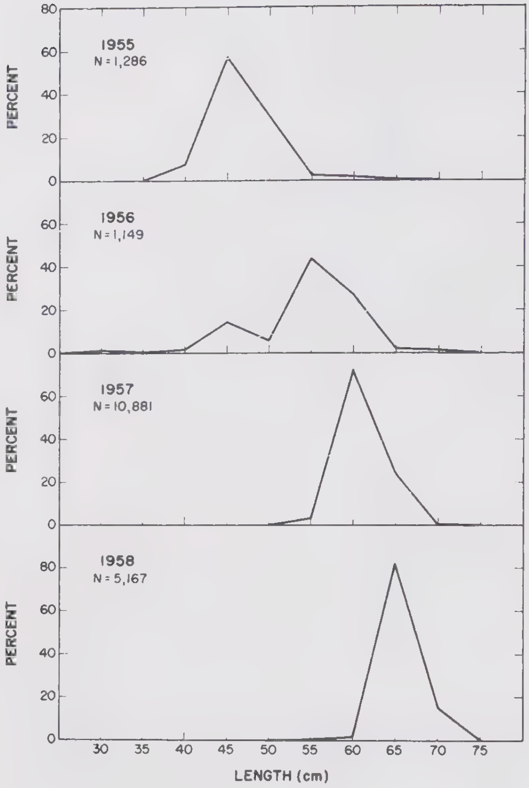

Figure 20.—Length-frequency distribution of *Sarda sarda* in the Black Sea, spring 1955-58. (Data from Mayorova and Tkacheva 1959, table 1.)

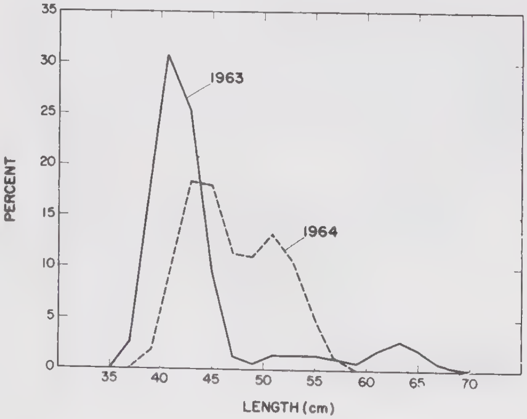

Figure 21.—*Sarda sarda* length-frequency distribution, Barbate and Tarifa, Spain. Data smoothed by formula $f_n = \frac{f_n + 2f_n + f_{n+1}}{4}$. (From Rodríguez-Roda 1966, fig. 11.)

year class) dominated the landings in May 1957. His sample showed that the May 1957 landings were composed of 10.5% age I fish (1956 year class), 28.7% age II fish (1955 year class), 53.2% age III fish (1954 year class), and 7.6% age IV fish (1953 year class). Mayorova and Tkacheva (1959) noted that a rich year class in 1938 also dominated the fishery in the Black Sea from 1938 to 1945.

The 1963 length-frequency distribution of *S. sarda* landed at Barbate and Tarifa, Spain, showed a strong mode centered at around 41 cm and lesser modes between 49 and 59 cm and 59 and 69 cm (Fig. 21). The 1964 sample had only two modes: one at about 43 cm and the other at about 51 cm. Rodríguez-Roda (1966) also presented a weight-frequency distribution of *S. sarda* (Fig. 22), which showed only two modes for the 1963 sample and only one well-defined mode for the 1964 sample. The 1964 data were also summarized by month (Fig. 23). The length-frequency distribution showed two well-defined modes in May, June, and July whereas the weight-frequency distribution showed only a single mode during those months. It is of interest that the relative proportion of fish in the larger mode in the length-frequency distribution appeared to decrease from May to July. The

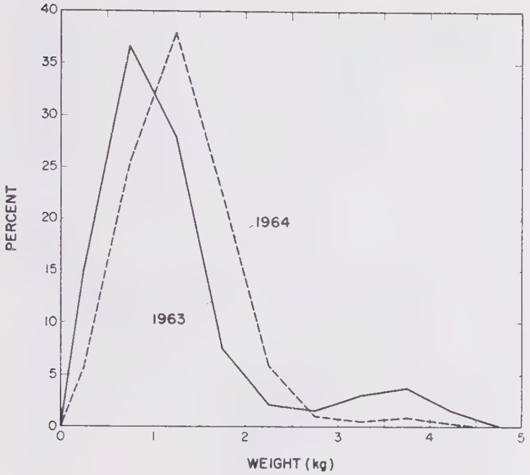

Figure 22.—*Sarda sarda* weight-frequency distribution, Barbate and Tarifa, Spain. Data smoothed by formula $f_n = \frac{f_{n-1} + 2f_n + f_{n+1}}{4}$ (From Rodríguez-Roda 1966, fig. 14.)

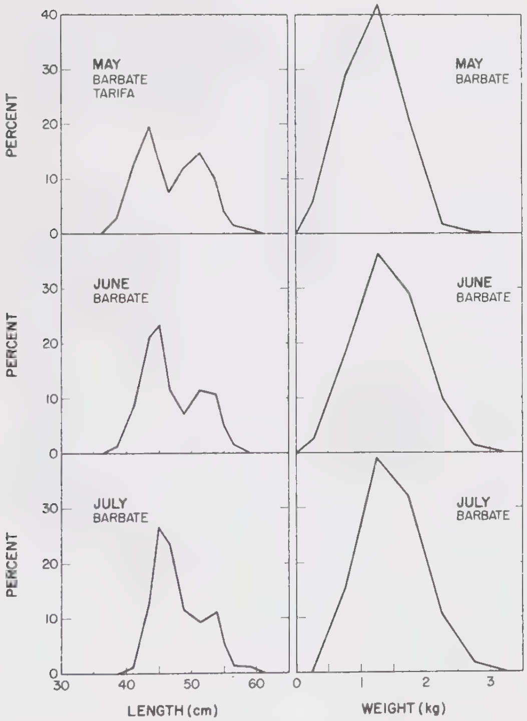

Figure 23.—*Sarda sarda* length (Barbate and Tarifa) and weight (Barbate) frequency distribution 1964. (From Rodríguez-Roda 1966, figs. 12, 15.)

length-frequency distribution of male and female *S. sarda* were similar except that the modes were displaced (Fig. 24).

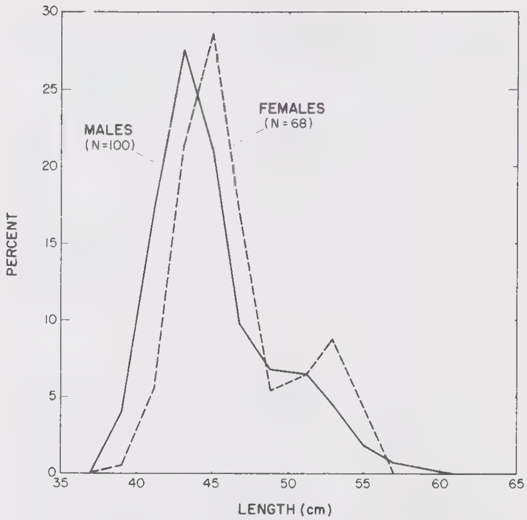

Figure 24.—*Sarda sarda* length-frequency distribution, Barbate and Tarifa, Spain, arranged by sex. (From Rodríguez-Roda 1966, fig. 13.)

Postel (1955a) presented data on the maximum size of *S. sarda* sampled in monthly periods in the eastern tropical Atlantic. The maximum lengths ranged from 450 to 690 mm for the males and 443 to 714 mm for the females.

Rodríguez-Roda (1966) computed the length-weight relation of *S. sarda* landed at the southern Spanish port of Barbate (Table 23).

4.14 Subpopulations

It appears that the *S. c. lineolata* found off northern Mexico and southern California comprise a single homogeneous stock. Tagging experiments conducted by the California Department of Fish and Game indicate that the bonito does not make long migrations. Although some tagged fish have traveled as far as 600 miles, most of the tagged fish have been recaptured in the vicinity of release; fish that traveled long distances moved from Mexico to southern California waters in the summer and back to Mexican waters again in the winter (Frey 1971; Collins and MacCall 1977).

From all indications it appears that the Northern and Southern Hemisphere populations of *S. chiliensis* are completely separate with little or no interchange. They are geographically separated from each other and there are certain meristic and morphological differences between the two populations. For example, the Northern Hemisphere population of bonito averages more vertebrae than the Southern Hemisphere population (Vildoso 1963b; Kuo 1970; Collette and Chao 1975).

Some preliminary work has been done on *S. chiliensis* to determine if protein differences attributable to genetic variation could be useful in identifying population units. Barrett and Williams (1967) experimented with gel-electrophoresis of the soluble eye lens proteins of bonito in an attempt to find such genetically controlled differences. They did find polymorphisms of the soluble lens proteins for the bonito. They also calculated the gene frequencies together with their expected distributions and found conformity to the Hardy-Weinberg principles. However, Barrett and Williams also found that the distributions of the apparent phenotypes were related to the lengths of the bonito. They concluded, therefore, that ontogenetic factors caused the observed polymorphism and that gel-electrophoresis of the soluble eye lens proteins, under the conditions used in their experiment, was not a useful technique in differentiating population units of bonito.

Smith (1971) examined the electrophoretic patterns of nuclear lens proteins from *S. c. lineolata* and also found polymorphism in the protein patterns. He suggested that there could be another explanation, as stated by Eckroat and Wright (1969), for the observed distribution of phenotypes than that suggested by Barrett and Williams (1967). Eckroat and Wright (1969) suggested that two separate fractions inherited as present/absence differences could account for the distribution of the three phenotypes observed by Barrett and Williams (1967). If this situation obtained, then the distribution of the observed phenotypes would indicate that there were two different breeding populations represented in the catches sampled.

It is not clear whether the stocks of *S. c. chiliensis* off Peru and Chile are independent of each other or whether they form a single homogeneous population. The center of bonito abundance off Peru is from Chimbote to Pisco (Ancieta 1963), which is centrally located between the north and south borders of Peru. The center of abundance off Chile is closer to the northern boundary of Chile near Arica, Iquique, and Antofagasta (Barrett 1971). In other words, the stocks of *S. c. chiliensis* off the coasts of Chile and Peru are at least contiguous with each other. In his attempts at determining a stock production model for the Chilean bonito, however, Barrett (1971) apparently considered only the Chilean stock. He listed as one of his recommendations, however, that future studies should include a "determination of relation, if any, with the Peruvian fishery for bonito."

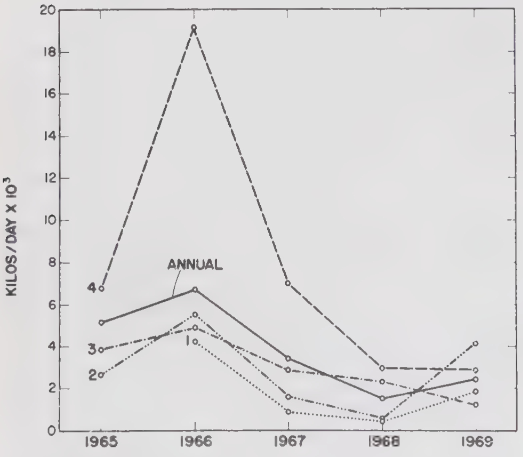

Figure 25.—Apparent abundance of *Sarda chiliensis chiliensis*, for individual quarters and years, by year, from data for the bonito vessels. (From Barrett 1971, fig. 8.)

No information is available on subpopulations of *S. orientalis* and *S. sarda*. The coastal distribution of all the species of *Sarda*, the migration patterns of *S. c. lineolata*, and the disjunct distribution of *S. orientalis* and *S. sarda* suggest the existence of discrete subpopulations. Based on scattered anatomical and meristic data, there appeared to be no difference in the populations of *S. orientalis*, although some morphometric differences were found in samples from Japan and the eastern Pacific. Similarly, a geographical comparison of *S. sarda* samples showed no conclusive differences among the various populations (Collette and Chao 1975).

4.2 Abundance and density

Sarda australis

Marshall (1964) said that *S. australis*, along the coasts of Queensland and New South Wales, are found in "great schools throughout the year." Grant (1972) stated that this species occurs in schools in Queensland waters especially during the winter months.

Sarda chiliensis

In the Chilean bonito fishery Barrett (1971) examined the relations among fishing effort, yield, and apparent abundance for the period from January 1965 to December 1969. Barrett recognized three different types of vessels, according to species objective, that fish bonito in the Chilean fishery: the anchovy, bonito, and tuna vessels. As the name implies, the anchovy and tuna vessels fished for bonito when anchovy and tunas, respectively, became less available and bonito more available. The bonito vessels fished primarily for bonito, although they did also capture other species. Barrett used the data from the bonito vessels for his analysis. The data for the entire monitored fleet, however, showed the same trends as for the bonito fleet after they were standardized to that of the bonito vessels. He noted a steep downward trend in total catch, an upward trend in relative fishing intensity, and a corresponding decline in apparent abundance in the fishery (Figs. 25, 26, 27). The trend appeared to level off in 1969. Barrett stated that the decline probably resulted from the effects of the fishery and not from fishery-independent factors.

MacCall et al. (1976) related the indices of abundance of the Northern Hemisphere *S. chiliensis* obtained by Squire (1972) on aerial surveys with catch per unit of effort (CPUE), in terms of catch in numbers of fish per angler, for the California party-boat fishery. MacCall et al. assumed that the aerial survey concentrated on the commercial fishing grounds because the surveys were

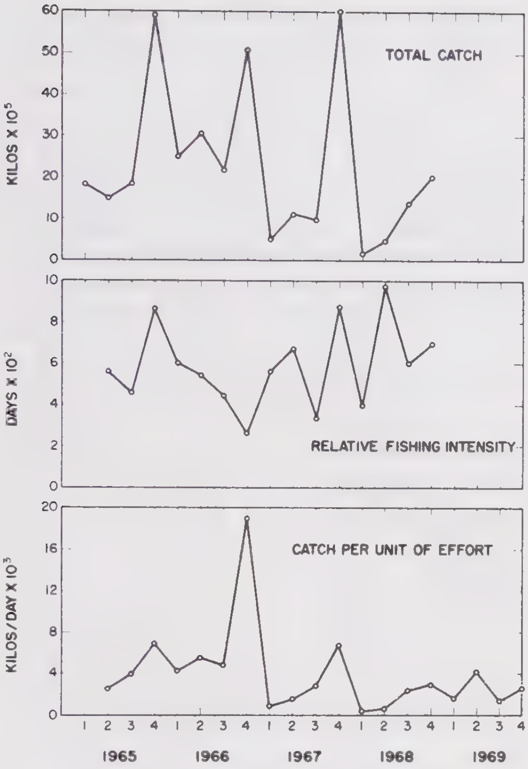

Figure 26.—*Sarda chiliensis chiliensis* total catch, and relative fishing intensity and apparent abundance (from data for the bonito vessels), quarterly from 1965 to 1969. Relative fishing intensity for 1969 is not shown because data for total catch in 1969 were not available. (From Barrett 1971, fig. 7.)

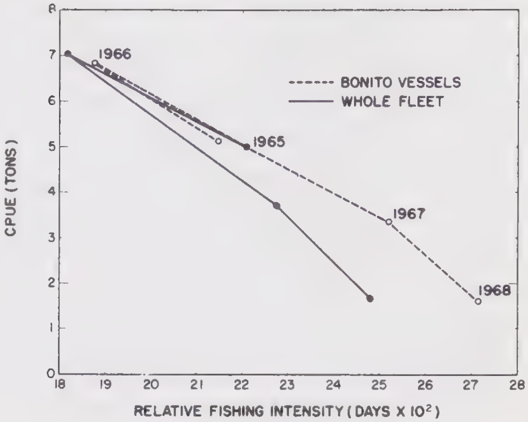

Figure 27.—Apparent abundance of *Sarda chiliensis chiliensis* in relation to relative fishing intensity from data for the bonito vessels only (dashed line) and for the fleet monitored by IFOP (Instituto de Fomento Pesquero) (solid line), 1965-68. (From Barrett 1971, fig. 9.)

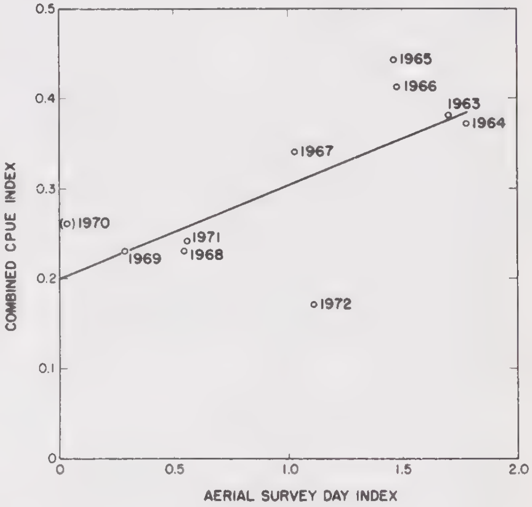

Figure 28.—Regression of aerial survey day index against CPUE adjusted for mortality and recruitment for *Sarda chiliensis lineolata.* (Note: Although the authors did not state how the line was fit, presumably, the least squares method was used.) (From MacCall et al. 1976, fig. 12.)

designed to aid the commercial fishery, and thus reflected changes in the stock occurring prior to exploitation by the commercial fishery. Also, since the length-frequency data showed that the party boats exploited younger bonito than the commercial fishery, they further assumed that the party-boat CPUE provided an index of prerecruit abundance of fish before they are exploited by the commercial fishery approximately 3 yr later. They computed a "combined" party-boat CPUE index which took into consideration mortality and recruitment and related it to the aerial survey day index for the period 1963-72 (Fig. 28). They concluded that the party-boat CPUE appears to be a valid indicator of recruitment to the commercially exploitable segment of the bonito stock, at least during this period. The party-boat CPUE from 1936 to 1973 indicated recruitment was very low before 1957, after which it increased sharply (Fig. 29) (MacCall et al. 1976). MacCall et al. further stated that *S. c. lineolata,* for unknown reasons unrelated to fishing, became scarce during the early 1940's and that subsequently and until 1956, the party boats were dependent on migratory fish. They noted that after 1956 ". . . large quantities of bonito moved into California waters and became re-established as a locally spawning population." During the 1960's young *S. c. lineolata* were abundant inshore and sports fishermen landed record numbers; however, since 1969 the sport catch has fallen drastically (Collins and MacCall 1977).

Sarda orientalis

The mean monthly landings and catch rates for *S. orientalis* in waters off southern Japan (Fig. 30) showed that

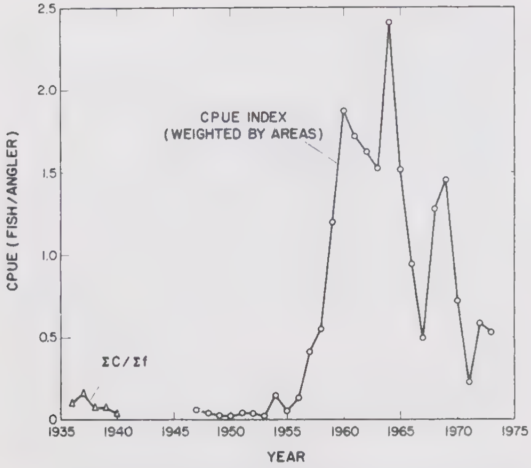

Figure 29.—Party-boat *Sarda chiliensis lineolata* CPUE as an index of annual recruitment. (From MacCall et al. 1976, fig. 13.)

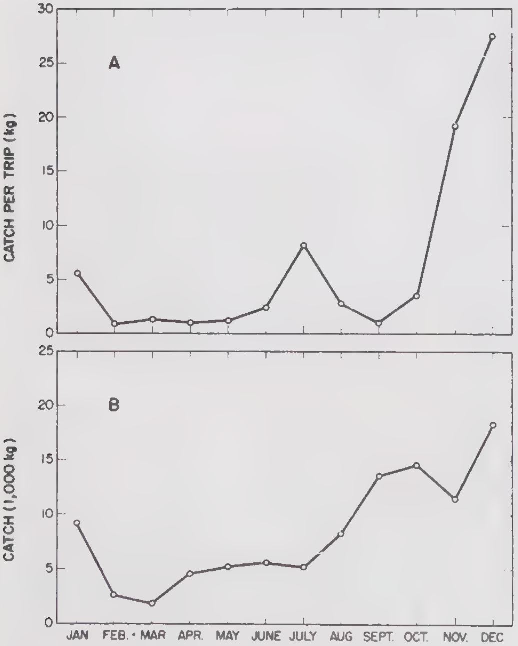

Figure 30.—Seasonal landings and catch rates of *Sarda orientalis* in southern Japan. A—Mean monthly catch per trip by trolling in the Aburatsu, southern Kyushu, Japan, fishery for *Sarda orientalis*, 1970-73. B—Mean monthly landings of *Sarda orientalis* at Tosashimizu and Muroto, Kochi, Japan, by various fishing methods 1967-73. (Data provided by S. Kikawa, Far Seas Fisheries research laboratory, and T. Koto, Nansei Regional Fisheries Research Laboratory, Japan.)

both the landings and catch per trip of *S. orientalis* were relatively higher during the fall-winter months, indicating that there are seasonal differences in the availability or abundance of *S. orientalis* off the coast of southern Japan.

Sarda sarda

Wide fluctuations in the landings of *S. sarda* in the Black Sea-Mediterranean Sea area are a characteristic of this fishery (Fig. 31), and investigators in this area have been trying to find the causes of the fluctuations. Artuz (1959) noted that the landings at the Istanbul fish market showed fluctuations following a 9-yr cycle during the period from 1936 to 1958 (Fig. 32). As stated earlier, part of the fluctuations were explained by the entry into the fishery of rich year classes. However, Mayorova and Tkacheva (1959) pointed out that although relatively good year classes develop in certain years, these fish fail

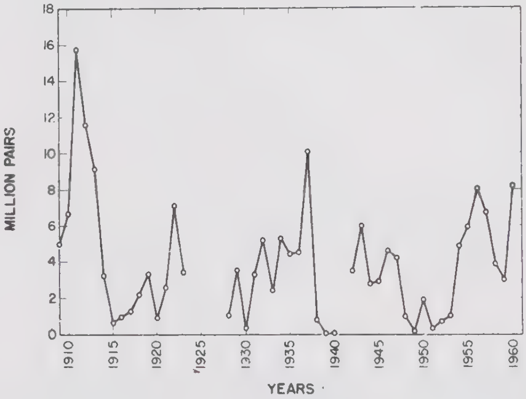

Figure 31.—The catches of *Sarda sarda* recorded at the Istanbul fish market, Turkey, 1909-60 (1 pair = two fish). (From Demir 1963, fig. 13.)

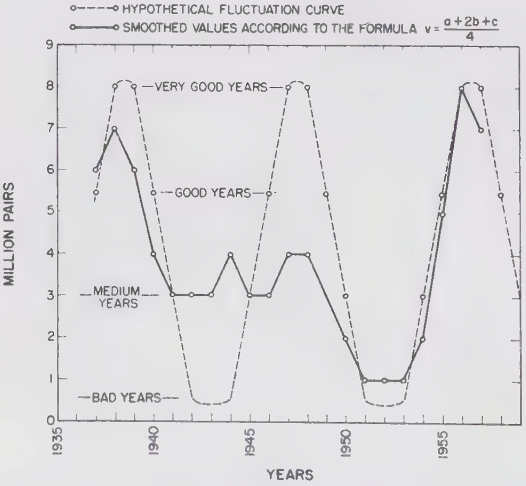

Figure 32.—Fluctuation pattern of *Sarda sarda* landed at the Istanbul fish market 1936-58. (From Artuz 1959, fig. 1.)

to return to the Black Sea. They concluded that ". . . the rich yield of young fish in the Black Sea is not always followed by an increase in the abundance of large pelamid."

Artuz (1959) also indicated a possibility of an inverse relation between the relative abundance of *S. sarda* and the mackerel, *Scomber scombrus,* in Turkish waters from 1940 to 1956 (Fig. 33).

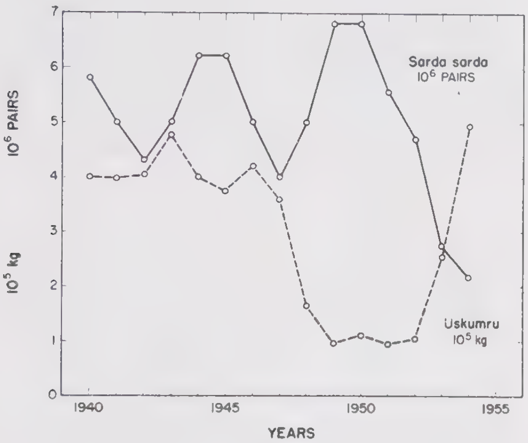

Figure 33.—Alternative occurrence of *Sarda sarda* (pairs) and uskumru, *Scomber scombrus,* (kg) landed from Turkish waters during the period 1940-56. (From Artuz 1959, fig. 5.)

4.5 Dynamics of population

Barrett (1971) was unsuccessful in developing a stock production model, following Schaefer (1954), for the Chilean bonito fishery. He cited as the cause of this the fact that the necessary assumptions for this type of model were unsatisfied. One of the requisite assumptions of the model is a stable age and size distribution in the population. The rapidly occurring changes in the fishery since 1965 have likely made this assumption untenable, according to Barrett. Another factor that affected the development of the model was the apparent discontinuous seasonal availability of some size classes of bonito in the fishery. Barrett concluded that he could not determine whether the fishery was stabilized or in a state of overfishing, and therefore recommended an accelerated research program on the Chilean bonito.

MacCall et al. (1976) developed a surplus production model for the Northern Hemisphere bonito in California waters (Fig. 34). They used total catch data and a combination of CPUE for the party-boat fishery and aerial survey index for the period 1963 through 1972 to develop the model. The model indicated that the Northern Hemisphere bonito is being harvested at or above the maximum sustainable yield. MacCall et al. cautioned, however, that the assessment was confounded by the possibility of a density independent decline in recruitment. They noted that the California catch of *S. c. lineolata* in 1973 appeared to be greatly in excess of the equilibrium yield. They stated, however, that conclusions drawn from the production model must be viewed with caution because bonito fishing in California waters is influenced by ocean temperatures.

Because of the lack of necessary data, MacCall et al. did not attempt a yield per recruit analysis.

Collins and MacCall (1977) determined a spawner-recruit relationship for *S. c. lineolata* during the period from 1964 to 1974 and found no simple functional curve to describe the relationship. They found that in some years a large spawning biomass was related to larger recruitment than did a small spawning biomass; however, in some years poor recruitment was also related to a high spawning biomass as well as to a low spawning biomass.

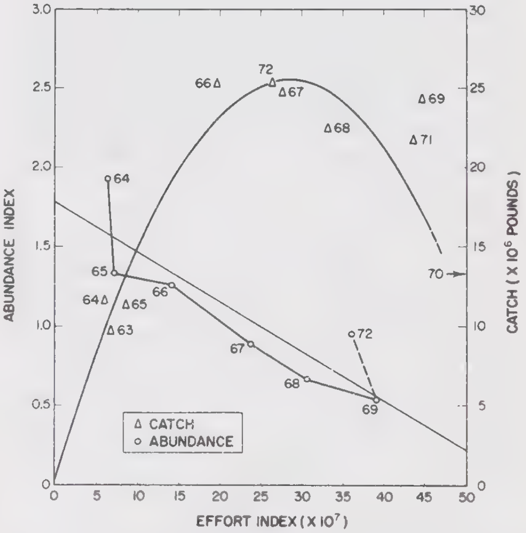

Figure 34.—*Sarda chiliensis lineolata* equilibrium yield and abundance in California waters. (From MacCall et al. 1976, fig. 14.)

4.6 The population in the community and the ecosystem

MacCall et al. (1976) analyzed trophic interaction between forage (northern anchovies, *Engraulis mordax,* and Pacific sardines, *Sardinops sagax*) and game fish (yellowtail, *Seriola dorsalis;* bonito, *Sarda c. lineolata;* albacore, *Thunnus alalunga;* barracuda, *Sphyraena argentea;* and white seabass, *Cynoscion nobilis*) in California waters. It appeared that there was little evidence that either forage or game fish biomass showed strong dependence on the abundance of the other. It appeared more likely that the abundance of both was determined largely by external conditions.

5 EXPLOITATION

5.1 Fishing equipment

Sarda australis

Sarda australis are generally taken incidentally by trollers who use the fillets as snapper bait or by sports fishers who use it as bait for billfishes and sharks (Grant 1972).

Sarda chiliensis

The California fishery uses various kinds of gear to catch *S. c. lineolata* including trolling gear and purse seine. The largest landings are made by the local purse seiners and the trolling fleet lands a lesser amount. The high-sea purse seiners may occasionally catch bonito to fill out the loads of other tunas (Frey 1971).

In a study of the California sport fishery it was found that *S. c. lineolata* made up the biggest part of the fish catch by a single species (Pinkas et al. 1968). Bonito are taken in party and private boats, from piers and jetties, and from the shoreline. They will strike at most bait and lures, and fishing techniques for bonito vary from still fishing to trolling.

The Chilean bonito fishery prior to 1964 was conducted almost entirely on an "artisanal, semi-industrial day-fishery basis" primarily from the ports of Iquique and Antofagasta (Barrett 1971). The vessels used in this fishery are known as "faluchos" and are about 10 m long. They fish principally with floating gill nets or with small purse seines called "boliches," which are hauled manually. During the period from 1964 to 1966, two modern 36 m tuna/bonito seiners and eight other bonito/tuna seiners entered the fishery. All the new purse seiners in the bonito fishery have power launches and power blocks and use nylon nets ca. 549-732 m (300-400 fathoms) long and ca. 73-110 m (40-60 fathoms) deep.

The fishing gear and vessels of the Peruvian fishery have been described by Ancieta (1963).

Sarda orientalis

In Japan this species is taken by various gear including trolling gear, pole and line, purse seines, and set nets. There is no exclusive fishery for *S. orientalis* in Japan; it is taken together with species that inhabit or enter the coastal waters of Japan in multispecies fisheries employing various gear. In the Philippines *S. orientalis* are taken mostly in traps (Warfel 1950). In the Indian Ocean fishery *S. orientalis* are taken primarily by drift nets (gill nets) in India and Sri Lanka.

Sarda sarda

Sarda sarda are taken by trap net, ring net, gill net, trammel net, purse seine, beach seine, and hook and line (Demir 1963).

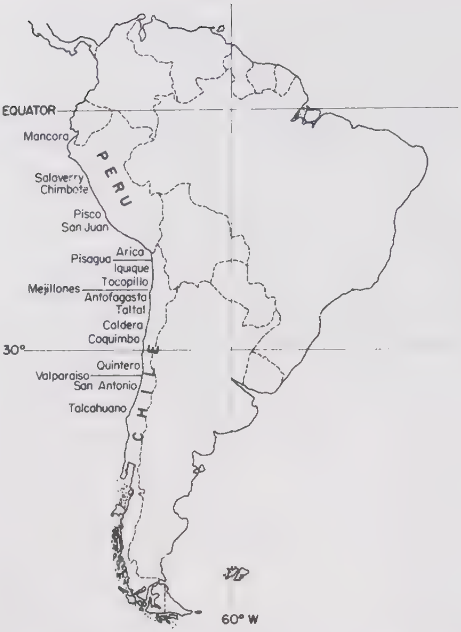

Figure 35.—Fishing ports of the Peruvian and Chilean fisheries for *Sarda chiliensis chiliensis*. (Adapted from Barrett 1971, fig. 1.)

5.2 Fishing areas

Sarda australis

There apparently is no well-developed fishery for *S. australis* in Australia. It occurs on the eastern coast of Australia along Queensland, New South Wales, and as far south as Port Fairy in Victoria. Serventy (1941a) stated that ". . . the bonito appears to be numerous enough to be regarded as a commercially important tuna, and a fishery could be maintained throughout the year on the eastern coast." Marshall (1964) noted that *S. australis* is destined to be of economic importance in Australia some day. There seems to be a difference of opinion on the food quality of *S. australis*. Grant (1972) stated that the flesh of the Australian bonito is dark red and its edible qualities are not highly regarded, whereas Marshall (1964) claimed that the flesh is light-colored, of delicate flavor, and of good canning quality.

Sarda chiliensis

The Northern Hemisphere *S. chiliensis* is most abundant in the area from Point Conception, Calif., to Magdalena Bay, Baja California (Frey 1971), and presumably this is the area in which the California-Mexico fishery for this species is conducted. Although the market for this species is limited, this bonito has been commercially fished in California waters since around 1900. However, the percentage of the California catch made north of the California-Mexico border has been declining. From 1965 to 1968, over 90% of the California catch was made north of the border; during 1969-74, it was reduced to 70%. There are two semi-independent *S. c. lineolata* fisheries in the northeastern Pacific: a southern California fishery conducted by small purse seiners and a fishery conducted by the high-seas tuna fleet in southern Baja California (MacCall see footnote 5).

The Southern Hemisphere population of *S. chiliensis* is exploited by the fisheries of Peru and Chile. The Peruvian fishery extends along the coastline from the port of Mancora (ca. lat. 04°S, long. 81°W) to the port of Ilo (ca. lat. 17°30′S, long. 71°15′W) (Ancieta 1963), and the Chilean fishery extends from Arica (ca. lat. 20°15′S, long. 70°15′W) to Talcahuano (ca. lat. 37°45′S, long. 73°W) (Barrett 1971) (Fig. 35).

Sarda orientalis

Fisheries for this species are not very well developed throughout its distributional range. The FAO Yearbook of Fishery Statistics (e.g., FAO 1974) does not show any *S. orientalis* landings. The *S. orientalis* found in the tropical eastern Pacific between central Baja California and Peru is of little commercial importance and when caught may enter the catch statistics grouped with *S. chiliensis* (Pinkas 1961). This species is uncommon around Hawaii, and when landed the catches are not identified in the statistics published by the State.

In Japan *S. orientalis* occurs in waters south of central Honshu along both the Pacific and Japan Sea coasts. It is most abundant in the coastal waters of Kyushu (Kikawa and Staff of the Nankai Fisheries Research Laboratory, Kochi, Japan 1963).

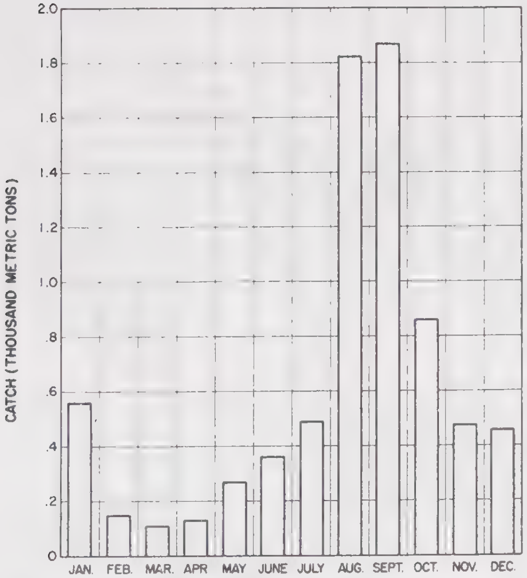

Figure 36.—Mean monthly landings and shipments into California of *Sarda chiliensis lineolata*, 1968-72. (Data from Heimann and Carlisle 1970; Pinkas 1970, 1974; Bell 1971; Oliphant and Marine Fisheries Statistics Staff. Marine Resources Region 1973.)

In the Indian Ocean minor fisheries for *S. orientalis* have been reported off the southwest tip of India (Silas 1964), in the Gulf of Aden along the coast of Somalia (Laevastu and Rosa 1963), and around Sri Lanka (Sivasubramaniam 1969).

5.3 Fishing seasons

Sarda australis

No information.

Sarda chiliensis

The mean monthly landings of *S. c. lineolata* in California for the 5-yr period from 1968 to 1972 indicate that the fishery is seasonal (Fig. 36). Although bonito was landed throughout the year in this 5-yr period, peak landings occurred in August-October.

Bonito is landed throughout the year in Chile and Peru, but both fisheries have seasonal peaks (Fig. 37). The seasonal peak is in October-November in Chile, whereas it occurs in January in the Peruvian fishery.

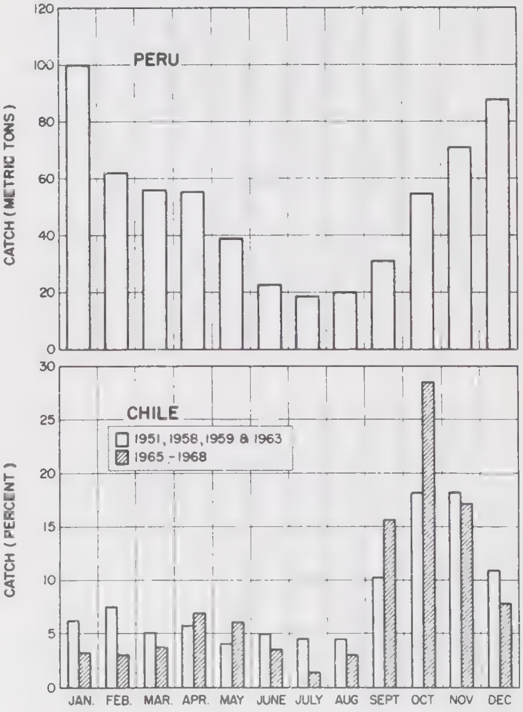

Figure 37.—Mean monthly landings of *Sarda chiliensis chiliensis* in Peru, 1951-59 (data from Ancieta 1963, table 1) and Chile (from Barrett 1971, fig. 2.)

Sarda orientalis

In the Indian fishery stray specimens may be taken in April, May, and June; however, the main fishing season appears to be from about July to September (Silas 1963). In nearby Sri Lanka, *S. orientalis* appears in the catches throughout the year off the south coast. Mature fish are taken along the northeast coast from June-August and off the south and southwest coasts between September and February. The juveniles appear off the west coast usually during the southwest monsoon in June-August (Sivasubramaniam 1969).

Sarda sarda

The fishing seasons for *S. sarda* in various areas are summarized in Table 8. Rodríguez-Roda (1966) summarized the fishing seasons in the Spanish fishery by various geographical areas in the eastern Atlantic and the western Mediterranean (Table 9). Apparently the fishing seasons in the Black Sea-Aegean Sea areas are related to the migrations of *S. sarda.* There is disagreement on the exact routes of the migration in certain areas, and the routes are unclear in other areas, but it is certain that *S. sarda* does migrate back and forth from the Aegean Sea, Sea of Marmara, and the Black Sea. According to Demir (1957), schools of *S. sarda* spend the summer in the Black Sea and the winter in the Sea of Marmara and the Aegean Sea. Thus, the fishing season of May-October coincides with the time the migrating *S. sarda* are in the Black Sea in the summer. The fishing peaks of April-May and September-December in the Sea of Marmara coincide with the spring migration of the bonitos from the Aegean Sea through the Sea of Marmara to the Black Sea and the fall return migration from the Black Sea to the Aegean Sea.

No information is available on the migration of *S. sarda* in the other areas of the Mediterranean and in the Atlantic Ocean. The seasonal development of the Spanish fishery in various areas of the western Mediterranean, however, suggests that *S. sarda* may be migrating to and from the western Mediterranean (see Table 9).

5.4 Fishing operations and results

The four species of *Sarda* are the bases of many fisheries throughout the world. Detailed information on the fisheries, however, is available only from a relatively few fisheries. *Sarda australis,* being found only along the coast of eastern Australia and around Norfolk Island east of Australia, is the object of a small incidental fishery in Australia. According to statistics published by FAO in the Yearbook of Fishery Statistics, *S. c. lineolata* is the basis of fisheries by Mexico and the United States. *Sarda c. chiliensis* is exploited by Chile and Peru. Landings of *S. orientalis* do not appear in the FAO Yearbook of Fishery Statistics (see FAO 1974). Relatively small amounts of the species are taken throughout its distributional range and it is not the basis of any well-developed fishery. *Sarda sarda,* on the other hand, appears to be exploited throughout its distributional range in fisheries of various sizes. In the Atlantic Ocean, the FAO Yearbook lists 18 countries reporting landings of *S. sarda,* mostly from the eastern Atlantic. Thirteen countries report landings of *S. sarda* from the Mediterranean and Black Seas. The total landings of *S. chiliensis* ranged from 53,300 to 94,100 t during the period 1965-73 and were greater than the total landings of *S. sarda* in each of 9 yr. The landings of *S. sarda* ranged from 25,000 to 65,700 t during the same period (Fig. 38) (FAO 1974).

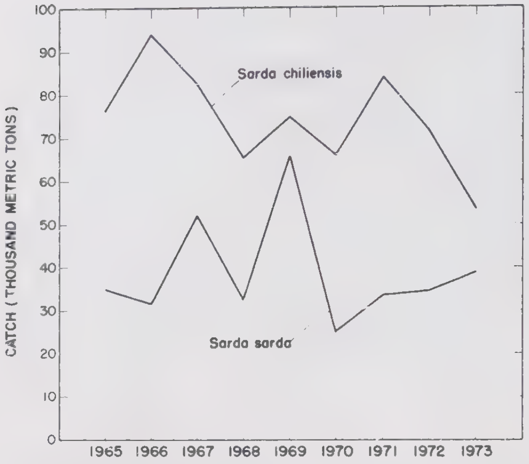

Figure 38.—Annual world landings of *Sarda chiliensis* and *Sarda sarda,* 1965-73. (Data from FAO 1974.)

Sarda australis

As can be expected from an incidental type fishery, the annual landings of *S. australis* were erratic and in some years no fish were landed at all during 1955-73 (Fig. 39). Information is meager on the utilization of the *S. australis* that are landed. They apparently are not uncommon in the wholesale fish market of Sydney, Australia (Collette[6]).

Sarda chiliensis

The landing figures of *S. c. lineolata* in California and Mexico show that Mexican landings make up only a small proportion of the total in the Northern Hemisphere (Fig. 40). From 1965 to 1973, the California landings constituted from about 77 to 100% of the total landings of bonito north of the equator in the eastern Pacific. The annual landings have been erratic, and to some

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[6] Collette, B. B., Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, D.C. 20560, pers. commun. February 1978.

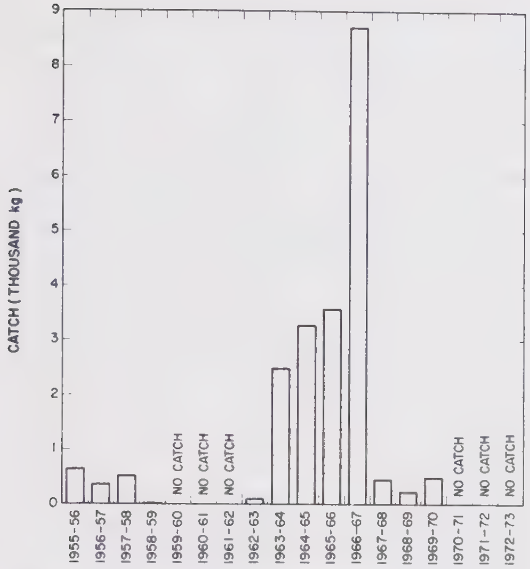

Figure 39.—Annual landings of *Sarda australis* in Australia. (Data from Australia. Fisheries Branch, Department of Primary Industry 1957-74.)

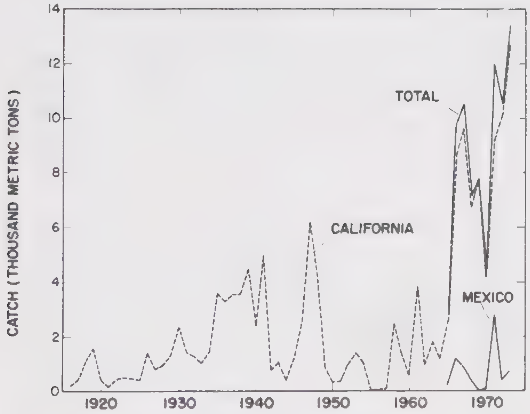

Figure 40.—California and Mexico landings of *Sarda chiliensis lineolata*. (Data from Bell 1971; Frey 1971; Oliphant and Marine Fisheries Statistics Staff. Marine Resources Division 1973; FAO 1974; Pinkas 1974.)

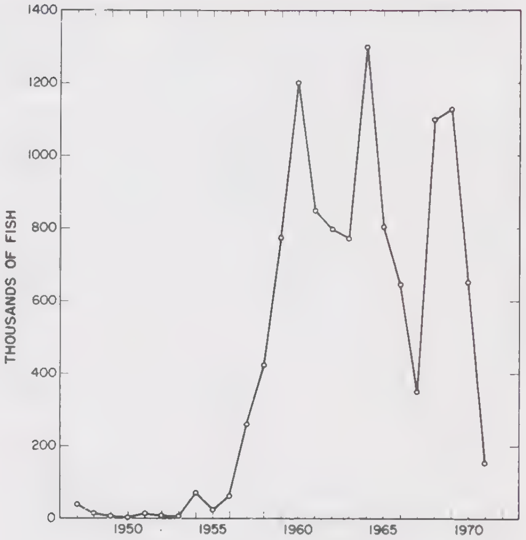

Figure 41.—Landings of *Sarda chiliensis lineolata* by the California party-boat fleet. (Data from Frey 1971; Oliphant and Marine Fisheries Statistics Staff. Marine Resources Region 1973.)

extent reflect the relative availability of the species in southern California and Mexican waters. It was believed that up until the early 1970's the landings did not reveal the condition of the stock because the bonito is caught incidentally or in lieu of more desirable species in the California fishery (Frey 1971). However, it is now believed that the recent small landings in California strongly indicate a low level of bonito abundance (MacCall see footnote 5).

The California party-boat landings of *S. c. lineolata* (Fig. 41) probably also better reflected the availability of bonito rather than the condition of the stock up until the early 1970's. The party-boat fishery is a multispecies fishery and many other species of fish in addition to the bonito are taken. Furthermore, the bonito is under a form of management in that sports fishermen may not possess more than 10 bonito/day. There is some indication that water temperature may affect the relative availability of bonito to the party-boat fishery in California waters. Party-boat landings of bonito were lower in the 6-yr period 1948-53, which were cold-water years in California (Young 1969). More recent data indicate that party-boat landings reflect the recruitment strength to the northern segment of the stock and therefore indicate the condition of the stock itself a couple of years later; also, catch per angler is a better measure of young fish abundance than is total landings (MacCall see footnote 5).

The landings of *S. c. chiliensis* in the fisheries of Peru and Chile (Fig. 42) indicate that the bulk of the landings is made in the Peruvian fishery. Chile's share of the Southern Hemisphere landings of bonito varied from about 2 to 15% of the total annual landings from 1965 to 1973. The annual Peruvian landings except for minor fluctuations increased steadily from 1941 and reached a peak of 104,000 t in 1961. The landings, with minor fluctuations, have been declining since then. Except for 1955, when the landings of bonito amounted to 7,500 t, the annual landings in Chile were <5,000 t during the period from 1940 to 1963. The landings increased sharply in 1965 and reached a peak in 1966 as the result of the entry of several new, modern purse seiners into the fishery in 1964-66 (Barrett 1971). They have, however, declined in subsequent years.

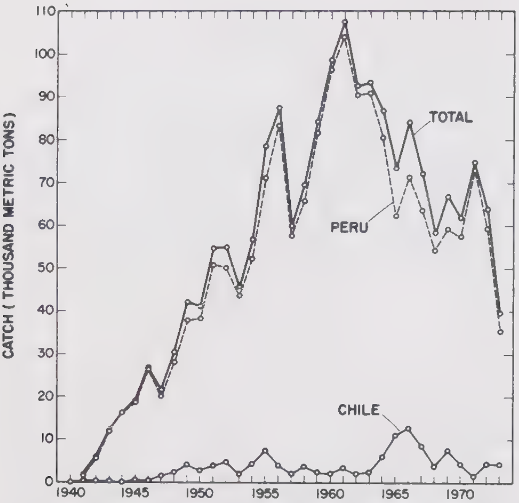

Figure 42.—Landings of *Sarda chiliensis chiliensis* in Peru and Chile. (Data from Ancieta 1963; FAO 1965, 1974; Barrett 1971.)

Sarda orientalis

The landings of this species are not identified in the statistics published by the Japanese Government. Apparently, landing records are maintained by prefectural "fishery guidance stations," but these statistics are presumably not published or not readily available.

Table 24 gives the annual landings made at four ports in southern Japan, Tosashimizu, Muroto, Murotomisaki, and Aburatsu, from 1967 to 1974.

There apparently is a minor fishery for *S. orientalis* in the Philippines. Warfel (1950) made a survey of the outlook for the development of a tuna industry in the Philippines. He presented some statistics showing the landings (number of fish) of *S. orientalis* at three Philippine markets: 369 at Batangas, 2,308 at Iloilo, and 6,762 at Zamboanga.

Sivasubramaniam (1969) concluded that the apparent abundance of *S. orientalis* around Sri Lanka was so low that it was not worth an attempt to develop a fishery for this species. He noted that not more than a few hundred pounds were taken in 1964 and estimated that the annual catch was about a ton in 1969.

Table 24.—Annual landings (in kilograms) of *Sarda orientalis* in four southern Japan ports. (Data provided by S. Kikawa, Far Seas Fisheries Research Laboratory, and T. Kato, Nansei Regional Fisheries Research Laboratory, Japan.) (ND = No data.)

Year	Landings in kilograms				
	Tosashimizu	Muroto	Murotomisaki	Aburatsu	Total
1967	37,462	ND	ND	ND	37,462
1968	22,171	ND	ND	ND	22,171
1969	30,024	ND	ND	ND	30,024
1970	30,718	ND	ND	25,461	56,179
1971	256,939	42,595	ND	31,732	331,266
1972	229,722	41,220	ND	9,994	280,936
1973	299,621	13,152	11,294	8,426	332,493
1974	ND	ND	11,710	ND	11,710

Sarda sarda

There are commercial fisheries of varying sizes almost throughout the entire distributional range of *S. sarda* in the eastern and western Atlantic and in the Mediterranean and Black Seas (Table 25).

Table 25.—Countries with fisheries for *Sarda sarda*. (Compiled from FAO 1974.)

Countries exploiting *Sarda sarda* in the eastern Atlantic:
- Angola
- Bulgaria
- Equatorial Guinea
- German Democratic Republic
- Greece
- Morocco
- Portugal
- Romania
- Spain
- U.S.S.R.

Countries exploiting *Sarda sarda* in the western Atlantic:
- Argentina
- Brazil
- Grenada
- Martinique
- Mexico
- United States
- Venezuela

Countries exploiting *Sarda sarda* in the Mediterranean and Black Seas:
- Algeria
- Bulgaria
- Cyprus
- Greece
- Italy
- Malta
- Morocco
- Romania
- Spain
- Tunisia
- Turkey
- U.S.S.R.
- Yugoslavia

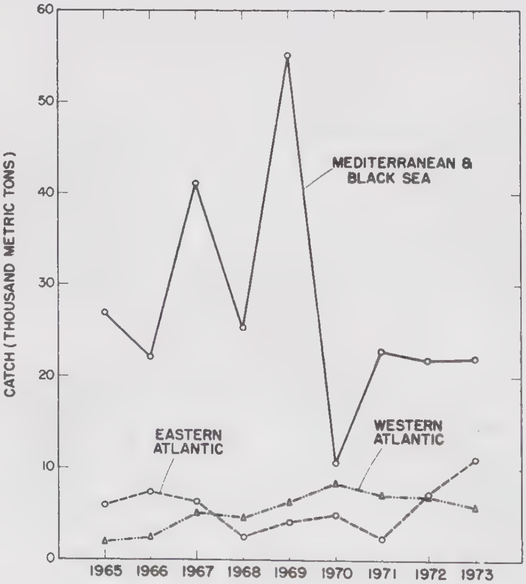

Figure 43.—Annual landings of *Sarda sarda* in the Atlantic and Mediterranean-Black Seas. (Data from FAO 1974.)

Table 26.—Annual landings of *Sarda sarda* (thousands of metric tons). (Data from FAO 1974.)

	1965	1966	1967	1968	1969	1970	1971	1972	1973
Eastern Atlantic:									
North	2.7	2.7	1.6	0.8	2.1	1.9	0.8	6.1	1.5
Central	1.9	3.0	3.0	1.3	1.2	1.9	0.9	0.5	9.0
South	1.3	1.6	1.7	0.4	0.9	1.2	0.7	0.6	0.5
Total	5.9	7.3	6.3	2.5	4.2	5.0	2.4	7.2	11.0
Western Atlantic:									
North	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
Central	0.3	0.4	0.5	0.8	0.8	0.7	1.0	1.2	1.8
South	1.5	2.0	4.6	3.8	5.4	7.6	6.1	5.7	4.0
Total	1.9	2.4	5.1	4.6	6.3	8.4	7.1	6.9	5.8
Mediterranean and Black Seas:	26.9	22.1	41.1	25.3	55.2	10.6	22.9	21.9	22.0

The annual landings of *S. sarda* in the eastern and western Atlantic and in the Mediterranean-Black Seas during the period from 1965 to 1973 show that except in 1973 when the eastern Atlantic landings exceeded 10,000 t, the landings in the eastern and western Atlantic never rose above this figure (Fig. 43, Table 26). The fisheries of Spain and Portugal make up the landings in the eastern Atlantic. In the western Atlantic the bulk of the landings is made by the fisheries of Argentina and Brazil. The landings in the Mediterranean and Black Seas fluctuated from 10,600 to 55,200 t during the period from 1965 to 1973. Turkey contributed 71.7 to 91.3% of the annual landings during this period.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory measures

There are no measures regulating the commercial fisheries for any of the species of *Sarda*. The State of California imposes a bag limit of 10 *S. c. lineolata* per day for recreational fishermen (Frey 1971), and is presently seeking to impose regulations on the California commercial fishery (MacCall see footnote 5).

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